

THESIS

DISTURBANCE PROMOTES NATIVE BEE BIODIVERSITY IN A SOUTHWESTERN PONDEROSA PINE
FOREST

Submitted by

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ABSTRACT

DISTURBANCE PROMOTES NATIVE BEE BIODIVERSITY IN A SOUTHWESTERN PONDEROSA PINE FOREST

Native bees are critical components of ecosystems where they provide an estimated 85% of pollination services. In recent decades, reports of global decline in bee populations have drawn concern from conservationists, compelling the need for further research on the drivers and mechanisms influencing the diminishment of native bee populations.

In ponderosa pine ecosystems, land management tactics of the late 19th and early 20th century, particularly fire suppression policies, promoted dense stand structures with closed canopies, a suppressed understory, and increased surface fuel loadings. Forest restoration practices including thinning of stands and re-introduction of fire are utilized as a technique to restore historical ecosystem structures, and restoration goals in southwestern ponderosa pine forests may align with conservationists' goals of creating desirable habitat for bees by promoting resource patch connectivity, growth of understory floral species, and landscape heterogeneity. However, despite the widespread implementation of ecological restoration tactics in western forests, the effects of restoration and disturbance in general on native bee communities are not understood but could have important consequences for ecosystem function.

To address this knowledge gap, the objectives of this thesis are: (1) describe the response of native bee communities to ecological disturbance, including wildfire, managed fire, and forest density reduction treatments, (2) identify structural components of ponderosa pine forests associated with site occupancy by native bees, and (3) inventory and describe the native bee fauna present in a common forest type of the Colorado Front Range.

In two separate studies, native bee communities were sampled within lower-montane ponderosa pine forest systems along the Colorado Front Range over a 2-year period. Sites were

representative of various wildfire severities (high and low) and forest management treatments (prescribed fire and mechanical thinning). I quantified bee α - and β -diversity and compared diversity metrics to variation in forest structure, foraging resources (floral abundance and richness), and nesting habitat (woody material). In total, 2,177 bee specimens were collected. Overall γ -diversity consisted of 5 families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), 25 genera, and at least 57 species. Four main findings emerged: (1) bee species richness and diversity varied across disturbance types and were highest within 1-year post-fire and high-severity wildfire stands, (2) unique bee community compositions were associated with different disturbance types but also varied across the growing season, (3) treatment type (non-treated, thinned, or burned) was associated with differences in bee functional variation, especially nesting behavior, and (4) floral resource abundances and richness were associated with increased bee abundance, richness, and α -diversity, though stand basal area was negatively correlated with bee abundance and species richness. These collective findings have implications for forest management and indicate structural elements of ecosystems that can be managed for enhancing bee biodiversity.

The data presented in this thesis provide evidence that fire-disturbed forest stands generally promote bee site occupancy compared to non-burned control stands, but this effect is likely to peak shortly after fires and then decline. In addition, distinct bee assemblages were found in stands that experienced different disturbances (e.g., thinned vs. burned vs. non-disturbed), indicating that a mosaic of disturbance histories is likely to support the greatest bee biodiversity at a landscape-scale. Further, findings here elucidate habitat structural components, specifically stand basal area and floral resource richness, that can be targeted by land managers to facilitate site occupancy by bees. Accordingly, I conclude that forest restoration practices including thinning and prescribed fire use, as well as natural fire disturbances, likely promote pollinator abundance and diversity (and ostensibly pollination services) in semi-arid ponderosa pine forests of the southwestern United States.

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DEDICATION

For the realm & my family matriarch, Phyllis Jean Schell [1928-2021].

TABLE OF CONTENTS

ABSTRACT ii

ACKNOWLEDGEMENTS iv

DEDICATION v

LIST OF TABLES vii

LIST OF FIGURES viii

CHAPTER 1: COLORADO BEES AND TREES 1

CHAPTER 2: THE α - AND β -DIVERSITY OF NATIVE BEE COMMUNITIES IS DRIVEN BY DISTURBANCE-MEDIATED SHIFTS IN STAND STRUCTURE, FLORAL RESOURCES, AND NESTING SUBSTRATES IN A SOUTHWESTERN PONDEROSA PINE FOREST..... 9

CHAPTER 3: PRESCRIBED FIRE USE PROMOTES NATIVE BEE BIODIVERSITY IN A SEMI-ARID FOREST ECOSYSTEM 37

CONCLUSION 62

LITERATURE CITED 65

LIST OF TABLES

CHAPTER 2

Table 2.1. A summary of all bee specimens captured (γ -diversity) per disturbance type, arranged by taxonomic designation (genus-level).....26

Table 2.2 Summary of a generalized linear model to describe variation in bee assemblages due to effects of forest structure and foraging habitat. Significant ($P < 0.05$) and marginally significant ($P < 0.10$) effects are bolded.....27

Table 2.3. A summary of all *Bombus* specimens captured per disturbance type.....28

CHAPTER 3

Table 3.1. A summary of bee genera captured in this study and their abundances by treatment type (i.e., time-since-fire and non-treated control stands).

Table 3.2. Summary of a generalized linear model analysis to describe variation in bee assemblages due to effects of forest structure and foraging habitat. Significant ($P < 0.05$) effects are bolded.

Table 3.3. A summary of all *Bombus* species captured per treatment type.

LIST OF FIGURES

CHAPTER 2

Figure 2.1. Map of study sites (Boulder County, CO) labeled (control plots indicated by blue, high severity plots in red, low severity plots in orange, thinned plots in green), wildfire burn scars (in red), and thinning treatment areas (in green).....29

Figure 2.2. Distribution of stand structural attributes including (a) tree density, (b) stand basal area, and (c) canopy cover (%). Characteristics of foraging habitat including (d) floral abundances, (e) floral species richness, and (f) 1000-hr surface loading were also quantified. Lettering denotes Tukey’s HSD test.....30

Figure 2.3. Relationship between 1000 hr fuel loading and (a) mean floral abundance, (b) mean floral species richness; Relationship between 1000 hr fuel loading and (c) mean floral abundance and (d) mean floral species richness with outlier plot removed. Both regression models are significant at a Type I error rate of $\alpha = 0.05$31

Figure 2.4. The distribution of (a) mean bee abundance, (b) mean bee richness, and (c) mean bee diversity (H') across disturbance type. Lettering indicates Tukey’s HSD test, and boxplots not connected by the same letter in each panel are significantly different.....32

Figure 2.5. The distribution of (a) bee abundance, (b) richness, and (c) diversity compared between high and low severity fire stands. Asterisk denotes a significant difference ($P < 0.05$) between sample means, with the cross symbol signifying a marginally significant difference ($P < 0.10$).....33

Figure 2.6. Sample-based accumulation of bee species diversity within disturbance types with Hill’s numbers representing (a) species richness ($q = 0$), (b) Shannon’s diversity ($q = 1$), and (c), Simpson diversity ($q = 2$). Shading represents the bootstrap-estimated 95% confidence interval for each sampling curve.....34

Figure 2.7. Ordination of bee community assemblages (NMDS), (a) compared between disturbance types and (b) sampling periods.....35

Figure 2.8. Relationship between bee abundance and (a) 1000-hr fuel surface loading and (b) stand basal area; bee species richness and (c) 1000-hr fuel surface loading and (d) 100-hr fuel surface loading; bee diversity and (e) floral abundance and (f) stand basal area. All regression models are significant at a Type I error rate of $\alpha = 0.10$36

CHAPTER 3

Figure 3.1a. Map of sites at Red Feather Lakes, CO with plots labeled and prescribed burn treatment area denoted (in green).....52

Figure 3.1b. Map of sites at Ben-Delatur Scout Ranch, CO with plots labeled and prescribed burn treatment area denoted (in green).....53

Figure 3.2. Distribution of bee foraging habitat across (a) collection period and (b) treatment type. Lettering denotes Tukey’s HSD test; boxplots not connected by the same letter differ significantly in mean value.....54

Figure 3.3. The distribution of (a) mean bee abundance, (b) mean bee richness, and (c) mean bee diversity (Shannon’s H' statistic) due to the effects of prescribed fire treatment. Lettering indicates Tukey’s HSD test, and boxplots not connected by the same letter in each panel are significantly different.....55

Figure 3.4 . The distribution of (a) mean bee abundance, (b) mean bee richness, and (c) mean bee diversity (H') across collection period. Lettering indicates Tukey’s HSD test, and boxplots not connected by the same letter in each panel are significantly different.....56

Figure 3.5. Sample-based accumulation of bee species diversity within treatment types with Hill’s numbers representing (a) species richness ($q = 0$), (b) Shannon’s diversity ($q = 1$), and (c), Simpson diversity ($q = 2$). Shading represents the bootstrap-estimated 95% confidence interval for each sampling curve.....57

Figure 3.6. Ordination of bee community assemblages (non-metric multi-dimensional scaling) across (a) collection period and (b) treatment type.....58

Figure 3.7. Mosaic plot illustrating ratios of observed nesting behavior among captured bees within each (a) collection period and (b) treatment type.....59

Figure 3.8. Linear models describing the relationship between bee abundance and (a) stand basal area and (b) floral species richness; bee species richness and (c) stand basal area and (d) floral species richness; and (e) bee diversity and floral richness. All regression models are significant at a Type I error rate of $\alpha = 0.05$60

CHAPTER 1: COLORADO BEES AND TREES

Introduction to native bee decline

Wild insect pollinators, particularly native bees, are critical components of healthy ecosystems where they influence plant community structure, maintain ecological networks (Loveless and Hamrick 1984), and provide pollination services to ~85% of wild and cultivated plants (Ollerton et al. 2011). Globally, ~3-8% of global crop production depends on insect pollination (Aizen et al. 2009), with a value of \$3.08 billion attached to pollination services provided by native bees alone (Losey and Vaughn 2006). Recently, research has suggested a widescale decline in native bee populations (Cameron et al. 2011), drawing concerns around long-term ecological and economic impacts (IPBES 2016) and warranting further exploration in understanding drivers of this decline. Recent literature increasingly recognizes pollination services are driven by landscape-level factors, with natural systems containing specific nesting and foraging resources (Potts et al. 2005; Landsman 2019). However, varying structural conditions of natural systems can alter bee habitat, creating cascading effects that directly affect bee site occupancy.

In Colorado and southwestern forests of the U.S., exponential population growth has exacerbated anthropogenically-driven impacts on forested systems (Savage 1991; Potapov et al. 2017). Land use conversion and intensification is a primary driver of decline among insect pollinator (Winfree et al. 2009; Potts et al. 2010), especially within the 'wildland-urban interface' (Radeloff et al. 2005) where conflict between ecological and human values heavily influence ecosystem management. The encroachment of anthropogenically intensive land into forested landscapes has led to expulsion of ecological disturbance processes in populated areas (Stephens and Ruth 2005). Notably, widespread fire suppression within the western U.S. has altered historical fire regimes and encouraged undesirable shifts within ecosystems. Within semi-arid ponderosa pine (*Pinus ponderosa* Lawson x Lawson) forests, which have typically experienced frequent, low-severity surface fire events, the absence of fire has created uncharacteristically dense stands across large spatial scales over the past century (Allen et al. 2002; Moore et al. 2006). These shifts in forest structure present numerous concerns to land managers

as high-density stands lead to suppressed understory productivity (Covington and Moore 1994), accumulation of surface and vertical fuel loadings, and higher probability of high-severity fire events (Fulé 1997).

To acknowledge these structural shifts, land managers have shifted their practice to an ecological restoration framework (Addington et al. 2018). Despite the generally beneficial effects restoration treatments may have on forest vegetation, the effects on native bee communities due to shifts in forest conditions are not well-understood and may prove to be beneficial or deleterious to bee populations. Additionally, forest bee communities are relatively understudied compared to agricultural and urban environments, with few studies available to reference when making management decisions within forested systems. To address this knowledge gap, objectives of this thesis are to: (1) describe the response of native bee communities to ecological disturbance, including wildfire, managed fire, and forest density reduction treatments, (2) identify structural components of ponderosa pine forests associated with site occupancy by native bees, and (3) inventory and describe the native bee fauna present in a common forest type of the Colorado Front Range.

Colorado bee taxa and life history strategies

Within Colorado, 946 bee species have documented distributions (Scott et al. 2011) - approximately a quarter of the ~4,000 described species found in North America (Wilson and Carril 2015). This high diversity can be generally attributed to the exorbitant differentiation of habitats across the state's elevational gradient, with Colorado's highest systems occurring at 1,012 m (3,320 ft) and highest systems reaching 4,399 m (14,433 ft). Across this gradient, a variety of environments including shrubland, grassland, woodland, montane forests, subalpine and alpine ecosystems exist (CNHP 2020), giving rise to unique floral communities which in turn further supports bee biodiversity. With this biodiversity, a wide array of bee morphologies and life history strategies are expressed, including explicit differences in sociality, nesting strategies, and foraging behavior.

Sociality

Bees exhibit various social behaviors, including solitary, semi-social, para-social, eusocial, and parasitic (Michener et al. 2000) with most bee taxa demonstrating solitary behavior (Batra 1984) and less than 10% of bees considered eusocial (Danforth et al. 2019).

Solitary bees compose approximately 85-90% of described bee taxa, comprising the majority of the world's bee diversity (Danforth et al. 2019). With this sociality, adults typically interact only during mating and when foraging for resources such as pollen and nectar. The female solitary bees solely construct nests, care for offspring (provide stored food resources), and lay eggs, though parental care throughout offspring development is often absent as parents typically die before maturation (Michener et al. 2000). Aggregated nests, where individual burrows are constructed in proximity, are not uncommon though females still tend to independently construct and tend to their own nests (Danforth et al. 2019). Examples of Colorado solitary bees include all of family Colletidae, most Megachilidae, most Andrenidae, some Halictidae, and a few genera in Apidae (Scott et al. 2011).

Within sub-social groups of bees, female behavior is similar to that of strictly solitary bees, though the females may provide limited parental care through actively providing food (rather than storing), defending nests, and co-existing with developing offspring (Michener et al. 2000). Examples of taxa that express this behavior include carpenter bees within genera *Xylocopa* Latreille and *Ceratina* L. (Scott et al. 2011).

Parasocial bees nest in small groups or colonies of individuals, consisting of an adult and a single generation of offspring (Michener et al. 2000). Within parasocial bees there are three subcategories of behavior: communal, quasi-social, and semi-social (Scott et al. 2011). Among communal bees, females co-inhabit the same nest though each bee constructs their own cells for their eggs. In quasi-social bees, females occupying the same nest cooperatively provide food for cells. Among semi-social bees, distinct divisions of labor are present with some females laying eggs and others provisioning offspring (Michener et al. 2000). Parasocial bee taxa within Colorado include some genera in Halictidae and Apidae (Scott et al. 2011).

Eusocial bees are those that form colonies, demonstrate cooperative brood care, have distinct division of labor, and produce overlapping generations that collectively maintain the colony.

Eusociality can be further divided into two sub-groups: primitively eusocial and highly eusocial (Wilson and Carril 2015). Primitively eusocial bees have annual colony cycles with colonies not persisting through periods of bee inactivity, in Colorado this being the cold months of winter. Most bees in the genera *Bombus* L. (bumblebees) are known for this behavior. Contrarily, highly eusocial bees have colonies that persist perennially (Michener et al. 2000). The only known highly eusocial species with established distributions in Colorado is the non-native Western honeybee, *Apis mellifera* Linnaeus (Scott et al. 2011).

Parasitic bees comprise about 15% of known bee taxa (Scott et al. 2011) and are often divided into two distinct subgroups: cleptoparasitic and socially parasitic. Female cleptoparasitic bees, or cuckoo bees, seek out host bee nests and will either 1) lay their own eggs among the host bee's eggs to exploit host bee provisional care, or 2) force host bees out of their nests to occupy it themselves (Michener et al. 2000). Examples of cleptoparasitic bees in Colorado include those in genera *Coelioxys*, *Sphecodes*, *Stelis*, and *Melecta* (Scott et al. 2011). Among socially parasitic bees, females 'take over' colonies of host bees, functionally replacing the host queen by laying her own eggs which are then provisioned for unknowingly by the host workers. In Colorado, bumblebees in the subgenus *Bombus* (*Psithyrus*) parasitize other species of bumblebees (Scott et al. 2011).

Nesting strategies

Nesting behavior among Colorado bees can be divided into two categories: below-ground nesters and above-ground nesters. Most solitary and social bees within Colorado create homes below-ground by burrowing into soil substrates. Some species utilize existing burrows, such as rodent nests or other insect-curated tunnels. Below-ground nesting bees found in Colorado include those in family Andrenidae, Melittidae, most Halictidae and Apidae, and some genera of Megachilids (Scott et al. 2011). A smaller division of bees are attributed to be above-ground nesters, often establishing nests in woody material such as standing trees, fallen logs, or stem piths. Burrows may be pre-established by other organisms, such as boring-beetles or wasps, or female bees may work to create homes themselves. Examples of above-ground nesting bees include those found in genus *Hylaeus* Fabricius and most Megachilids (Scott et al. 2011).

Foraging behavior

Bees are obligate-flower visitors whose evolution has been driven by that of angiosperms' (Danforth et al. 2019). The immature stages of bees rely on pollen and nectar as their source for vital nutrients, primarily protein and carbohydrates. Adult bees, male and female, forage to nourish themselves though most foraging efforts are directed at provisioning brood cells (Michener et al. 2000). Floral oils may also be utilized for nutrition and nesting material, though this is rarely observed.

Most bees are polylectic, or generalist foragers, collecting pollen from a wide variety of flowering plant species and across various plant families. Polylectic species do not have host plants that they rely on specifically for their life cycles, leading to broad distributions of species and extended periods of activity throughout the growing season. Colorado polylectic species include *Bombus*, *Apis*, and some groups of Halictids and Xylocopids (Scott et al. 2011). Contrastingly, oligolectic foragers tend to be specialists and collect nutritional resources from a single plant taxon, typically a genus rather than a single species (Cane and Sipes 2006). Oligolectic species in Colorado are found within the genus *Andrena* F. and the families Megachilidae and Apidae (Scott et al. 2011).

Collections and documentation

Current Colorado bee collections illustrate bias across with disproportion sampling having occurred across the state. The highest documentation of species has occurred primarily within Northern Colorado and along the Front Range, particularly in Boulder and Larimer County (Scott et al. 2011). This can be attributed to these counties being home to the state's two largest universities: Colorado State University (Fort Collins) and University of Colorado (Boulder). As a result, researchers from these institutes likely contributed ample amounts of species data to these regions through localized entomological studies. Additionally, Boulder and Larimer County both subsume large elevational gradients, ranging from grasslands at 1,389 m (4,557 ft) to alpine systems reaching 3,716 m (12,192 ft). Inclusion of such a large gradient in sampling efforts likely contributed to the documentation of high native bee diversity.

Yet, other areas of Colorado remain largely under-sampled with some counties having no published species data, including Colorado's eastern plains and southwestern region (Scott et al.

2011). The inclusion of these areas in future sampling efforts may lead to documentation of new species found within the state's borders as well as contribute new distributional data for previously collected species.

Forest management and native bee biodiversity

Southwestern ponderosa pine systems have evolved for centuries, driven by natural disturbance processes including frequent low-severity surface fires, insects and disease outbreaks, and climatic events such as drought (Allen et al. 2000). These disturbances assisted in the maintenance of heterogeneous forest structures across landscape. However, land management following European settlement in the late 19th and early-20th century led to alterations of these spatial structures through installation of fire suppression policies, livestock grazing, and logging, which promoted development of more homogeneous stand structure and stem densities. These unnaturally dense stands with increasingly dense canopies led to the decrease in abundance and diversity of vegetation communities (Covington and Moore 1994), loss of biodiversity (Allen 1998), and diminished connectivity between resource patches.

To acknowledge these shifts, practitioners are incorporating ecological restoration goals and incentives into management plans. In ponderosa pine forests, the goal of restoration treatments is to reduce stand densities through thinning operations to reflect historical conditions. These density reductions within forests are associated with higher ecosystem productivity, increased habitat connectivity, and greater resistance to high-severity fire events (Bailey and Covington 2002; Skov et al. 2005). Tree removal may be accompanied by the re-introduction of low-severity surface fires through controlled burns with the goal of reducing surface fuel loadings and initiating vegetative release. However, initiating such treatments on a large scale is often infeasible due to lack of funding and pushback from local communities where treatments are proposed (Schultz et al. 2019, Paveglio et al. 2009). This, cumulatively with burn scars left by wildfires, has led to a mosaic of habitat conditions across the landscape with forest stands in various structural conditions.

As these restoration treatments become more common practice in ponderosa pine forests, it is crucial to understand how practices impact native bee communities. Thinning and prescribed burns

may affect abundance and diversity of floral resources, nesting site quality and availability, and insolation levels (Allen et al. 2002), which may prove beneficial or detrimental to pollinating insect communities. Specifically, overstory thinning leads to decreases in canopy cover, increasing light filtration to the forest floor. Increased light availability allows greater opportunity for thermoregulation and promotes understory vegetative productivity (Nyoka 2010), improving foraging habitat for bees. For example, Hanula et al. 2016 found that in loblolly pine forests, tree basal area was a primary predictor of bee species diversity, whereas canopy openness and plant species richness were the most reliable predictor of bee abundances at the site-level. Comparatively, prescribed burns can consume surface debris including litter and woody fuels, creating trade-offs between bee taxonomical groups. Below-ground nesting bees may benefit from the increased exposure of bare soil substrate, whereas above-ground nesting bees who rely on woody debris or vegetation on the surface may experience declines in nesting habitat suitability. For instance, Ulyushen et al. 2021 found frequent prescribed fire generally improved nesting habitat for below-ground nesting bees in southeastern U.S. forests. Findings from Carper and Bowers 2017 also reveal a generally positive response between woody debris presence and bee site occupancy, with bee abundance decreasing by 40% as a result of woody debris removal.

In terms of wildfire, associated impacts on native bees have been relatively under-represented by research, with most studies studying post-fire response in the context of prescribed fires or lacking the spatial scale to fully encompass possible variation in fire severity (Galbraith et al. 2019a). Exceptions to this include a recent study by Galbraith et al. 2019a, which examined wild bee response to variation in fire severity in mixed-conifer forests of the U.S. Pacific-Northwest. Researchers found fire severity drove responses in bee diversity, with relative abundance of species shifting along a fire severity gradient. Another study by Ponisio et al. 2016 assessed the influence of pyrodiversity on insect pollinators in forest-scrublands and found positive effects of low to moderate-severity fire on pollinator communities. Further research can build off these initial findings with broadened scopes, in terms of both wildfire characteristics (severity, extent) and study ecosystems.

Though a foundation of literature exists that examines relationships individually between restoration and wildfire disturbance to native bee populations, comparative insight between disturbance types is lacking - particularly within southwestern ponderosa pine systems. This thesis will be among the first collection of studies to explore effects of thinning, prescribed fire, and mixed-severity wildfire on native forest bee biodiversity. Projects included here will examine multiple potential linkages between forest structure and habitat resources while providing suggestions on site-level controls of habitat characteristics for managers that are imperative to bee site occupancy. Findings here will contribute to a growing body of literature that will assist land managers in addressing goals for not only forest health, but pollinator conservation as well.

CHAPTER 2: THE α - AND β -DIVERSITY OF NATIVE BEE COMMUNITIES IS DRIVEN BY DISTURBANCE-MEDIATED SHIFTS IN STAND STRUCTURE, FLORAL RESOURCES, AND NESTING SUBSTRATES IN A SOUTHWESTERN PONDEROSA PINE FOREST

Overview

Within forested ecosystems, most flowering plants rely on native bees for the maintenance of ecological networks and the provisioning of pollination services. However, recent research supports large-scale pollinator declines, causing concern among conservationists and warranting a need to understand drivers of said decline. Within lower-montane ponderosa pine forested systems, habitat conditions have been altered due to forest management following western colonization in the late 19th century. Particularly, fire suppression has led to shifts in ponderosa forest structure to high tree densities and stifled understory production. To acknowledge these shifts, forest restoration practices have been used to assist with re-establishment of variation in ponderosa pine forests with the goal of returning fire to the landscape. However, little is known as to how variation in habitat structure and composition driven by disturbance, including ecological restoration and wildfire events, impacts native forest bees. Here, we developed three objectives to acknowledge this knowledge gap: (1) describe response of native bee communities to ecological disturbance, including forest management and wildfire, (2) identify structural components of ponderosa pine forests associated with native bee site occupancy, (3) inventory and describe native bees found along the Colorado Front Range.

Using blue vane traps, bee community assemblages were sampled across the growing season in 39 ponderosa pine forest sites in central Colorado to evaluate the effects of wildfire and forest thinning disturbances on native bee populations. We quantified bee abundance, richness, and diversity as well as foraging resources (flower abundance and richness) and nesting habitat (woody material). Four key findings emerged: (1) overall γ -diversity was high and consisted of 5 families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), 30 genera, and at least 70 unique bee species. Predominant genera consisted of bumblebees (*Bombus* spp.), mason bees (*Osmia* spp.), and

digger bees (*Anthophora* spp.), accounting for 50.5%, 9.2%, 5.3 % of all captures, respectively. (2) Average bee abundance did not vary across disturbance types, though bee species richness and α -diversity were highest in stand affected by high-severity wildfire. (4) Bee assemblages were different across disturbance type, such that bee biodiversity was highest in high-severity wildfire stands. (5) Various components of bee foraging, and nesting habitat were associated with shifts in bee community metrics. We conclude that thinning operations are not associated with reductions in bee abundances, richness, or diversity, and fire disturbances generate foraging and nesting habitats that are important for native bee diversity. However, community structures vary across disturbance types and specific assemblages tend to be associated with non-treated, thinned, and burned sites, indicating that managers can use thinning and burning treatments as tools for conserving bee biodiversity across the landscape.

Introduction

Native bees are critical components of healthy ecosystems, providing 85% of wild and cultivated plants with pollination services (Ollerton et al. 2011), which maintains ecological networks (Loveless and Hamrick 1984), promotes landscape level biodiversity (Potts et al. 2016), and improves yields in agricultural systems (Garibalid et al. 2013). Despite the importance of bee communities for ecosystem function, there is growing evidence of global decline in both wild and managed bee populations (Goulson et al. 2008; Potts et al. 2010), underscoring a need to understand the drivers and mechanisms of this decline and identify potential targets for conservation. It is recognized that landscape level factors such as proximity of natural ecosystems to managed systems and the fragmentation of habitats drive pollination services (Ricketts et al. 2008; Carvalheiro et al. 2010) and may influence bee distributions (Potts et al. 2006). However, it remains poorly understood how widely implemented ecosystem management efforts, especially ecological restoration practices, directly and indirectly affect native bee populations.

Disturbances, both natural and anthropogenic, are primary drivers of ecosystem composition, function, and structure across coniferous forest ecosystems (Franklin et al. 2002). In western North America, fire is a prevalent disturbance to which many forest communities are adapted. Historical fire

regimes have changed as a result of fire suppression policies over the past century; these changes have been further exacerbated by with global climate change (Miller et al. 2009; Dennison et al. 2014; Jolly et al. 2015). Although it is recognized that fire disturbances are important ecosystem processes, fire suppression has resulted in shifts to undesirable forest structures in many areas (Parsons and DeBenedetti 1979; Fulé et al. 2009). For example, lower-montane ponderosa pine (*Pinus ponderosa* Douglas ex Lawson) forests historically experienced frequent, low- to mixed-severity surface fire events prior to human settlement (Addington et al. 2018), which restricted recruitment of saplings into the overstory. The exclusion of fire from these systems has facilitated a widespread increase in stem densities with consequences for understory productivity, fuel loadings and vertical fuel structures, and the risk of severe fire events (Allen et al. 2002).

Ecological restoration is a tool used to address and mitigate these structural shifts. In ponderosa pine systems, the transition from high stem densities with uniform structure to low stem densities is achieved primarily through thinning operations (Allen et al. 2002). Such treatments incorporate the goal of reducing forest density and stand basal area to reflect historical stand conditions and increase resistance to high severity fire events by reducing available fuels in the overstory and understory (Bailey and Covington 2002; Addington et al. 2018), which may promote or detract from other ecosystem functions, including pollination. Recent work shows that site occupancy by native forest bee populations is indirectly promoted by reduced basal area: less canopy cover leads to recruitment of floral cover by increasing light availability at the forest floor, and bees respond to these resources (Eltz et al. 2002; Jha and Vandermeer 2010; Davis et al. 2020). Thinning practices may also alter woody debris availability, an important nesting resource for solitary bees in particular (Danforth et a. 2019), through the removal or creation of debris on the ground surface, further influencing bee site occupancy and potential pollination services. Despite these potential effects, no studies have examined the effects of thinning motivated by fire risk reduction on bee communities within southwestern ponderosa pine systems, and studies assessing the effects of fire disturbance are often limited to prescribed burn treatments (Campbell et al. 2007; Rodriguez and Kouki 2015; Simmons and Bossart 2020).

To address this knowledge gap, we ask the question “How do disturbances from wildfire and fuels reduction (thinning) treatments affect bee communities in ponderosa pine forests?” To answer this question, we tested the following hypotheses: (1) α - and β -diversity of bee assemblages differs among stands that recently experienced wildfire, stands managed with density reduction treatments, and non-treated, high-density stands; (2) thinning promotes bee abundance and diversity compared to non-treated control stands; (3) fire severity (‘low’ vs ‘high’ severity) has differential impacts on bee community abundance and diversity; and (4) differences in forest structure and foraging habitat relate to variation in bee community assemblages. Our study provides a new description of native bee biodiversity in ponderosa pine forests of central Colorado and insight into how anthropogenic and natural disturbances interact with site structural elements to predict variation in bee communities, with consequences for ecosystem management practices.

Methods

Study system

Bees were collected from 39 lower-montane sites (1655-2530 m elevation range) in central Colorado during the growing seasons of 2019 and 2020 using passive trapping methods (Fig. 2.1). Overstory vegetation in stands selected for study was predominantly ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), though lodgepole pine (*Pinus contorta* Dougl.) and Douglas fir (*Pseudotsuga menziesii* Mirb.) reached the overstory in some areas. Sites were selected to represent four different disturbance types including (1) high severity wildfire (stands that experienced almost complete overstory tree mortality, 80-100% tree mortality), (2) low to moderate severity wildfire (stands that burned but experienced overstory tree mortality between 10-79%), (3) forest density reduction treatments and (4) non-treated/non-burned control sites. Sites were selected as a subset of stands sampled and inventoried in Stevens-Rumann and Fornwalt (2018) where study site understory plant community assemblages were comprehensively described. Wildfire sites spanned three fires that occurred between 2010-2012 within Boulder County, CO. Stands that had undergone density reduction treatments had no recent burn history and were treated to reflect an average overstory basal area of $19.0 \text{ m}^2/\text{ha} \pm 2.0 \text{ m}^2/\text{ha}$ between 2009-2013 (Stevens-Rumann and Fornwalt 2018).

Bee sampling procedure

Due to variability within bee communities across the growing season (Rhoades et al. 2018), each site was sampled three times in each year of the study to reflect periods of peak bee activity including June 'early-season'; July 'mid-season'; and August 'late-season' (39 sites x 3 collection periods x 2 years = 234 collections total). Blue vane traps (Springstar, Inc. Woodinville, WA, USA) were hung during each collection period from existing vegetation at a height of ~1.3 m for 48 h during periods of favorable weather (low cloud coverage, no precipitation, average daily temperature above 22.2 °C). One trap was placed per site during collection events. Each trap included a wire mesh insert to provide refugia to trapped specimens in the case of unfavorable weather and three 1 mm drilled holes to reduce the probability of inundation with water. Upon the end of each sample period, trap contents were collected, placed on dry ice, and returned to the lab where all bees were pinned and identified to the lowest taxonomic level possible. In most cases this was genus and species, but some specimen could only be sorted to morphospecies (denoted 'sp. 1,' sp.2,' etc.). Voucher specimens are curated at the C.P. Gillette Museum of Arthropod Diversity at Colorado State University.

Forestry and understory measurements

At each collection location, site-level information on forest structure was collected on 0.01 ha fixed-area plots (10 m²). Bee passive traps were placed at the center of fixed area plots at each collection period to associate vegetation measurements with bee assemblages. On each plot, trees were censused and their diameter at breast height (dbh) was recorded, as well as species. Overstory canopy cover was collected along two 7.6 m transects running north and south from plot center using a densitometer. The presence of both live and dead overstory cover above breast height were tallied. Additional forest structure measurements were collected for a previous study on similar sites (see Stevens-Rumann and Fornwalt 2018). Briefly, all overstory trees (>1.4 m) were measured within 0.04-ha plots for species, live or dead status, diameters at breast height (dbh), and height. From this information, basic forestry metrics were computed and included as variables for analysis, including stand basal area (m²/ha), tree density (trees/ha), and overstory canopy cover (%).

In addition to forest structure characteristics, we measured site structural elements important to bee foraging and nesting. Coarse woody debris availability is an important predictor of potential nesting habitat, particularly for solitary bees (Rodriguez and Kouki 2015). To measure the availability of fine woody debris (both sound and rotting material on the ground surface <7.6 cm diameter; grouped into 1-hr, 10-hr, and 100-hr size classes), fuels planar transects (Brown 1974) were utilized to generate tally estimates. Transects originated at trap location in each site and extended for 10 m in each cardinal direction (40 m total transect length per collection site). Tallyed planar intercepts of fuels were aggregated across the four transects to provide a single site-level estimate of fine woody debris surface loadings for each size class. Coarse woody debris with diameters >7.6 cm (i.e. 1000-hr fuels) were measured within a 0.015-ha (6.9 m) fixed-area plot around the trap location. Diameters of both ends as well as length were recorded and included as a separate site-level estimate surface loading calculation in megagrams per hectare (MG/ha).

Floral resources are a primary predictor of bee site occupancy (Winfree 2010) and were included in our site inventory. At each collection period, floral abundances and species richness were measured as sites using quadrats. At each site and collection period, five 1x1 m² quadrats were deployed and the total number of active floral displays (number of individual flower plants, as determined from stem density) and number of unique species represented by active floral displays were recorded. One quadrat was placed directly beneath the trap location, with additional quadrats placed 2 m in each cardinal direction. Quadrat measurements were treated as a subsample, and values from all 5 quadrats at each site were averaged together to yield a site-level mean floral abundance and richness for each collection period.

Data analyses

All statistical analyses were conducted using the R programming language (V 3.5.2, "Eggshell Igloo"). A Type I error rate of $\alpha=0.05$ was used to assign statistical significance to modeled effects. However, effects that were significant at $\alpha=0.10$ were interpreted as 'marginally significant' to account for factors that may be ecologically important but were not classically 'significant' due to high variability present in ecological studies.

To compare forest overstory structure between sites that underwent thinning disturbance, low-severity fire, and high-severity fire, a one-way ANOVA model was used to compare mean basal area, mean tree density, and canopy cover (%). Mean floral abundance and number of species were also compared between disturbance types using an ANOVA model, accounting for sampling year as a random effect. Post-hoc contrast tests were utilized to determine 1) whether thinning treatments were associated with shifts in bee community assemblages relative to non-treated control sites, and 2) whether the effects of high severity fire on bee assemblages differ from those of low severity fire.

To account for variability in bee communities across the growing season, a two-factor ANOVA was used to analyze the fixed effects of site disturbance type (density reduction treatment, low-severity fire, high-severity fire, and non-treated control), seasonality (early, middle, and late), and the disturbance type \times seasonality interaction on the responses of mean bee abundance (number of bees), bee species richness (number of species), and bee α -diversity using the Shannon-Weiner diversity index (H' statistic). This analysis used site \times month \times year observations as the unit of replication ($N = 234$). Bee abundance data was log-transformed to conform to assumptions of normality prior to analysis. Since Shannon's H' cannot be calculated when no species are present ($H' = 0$ when a single species is present), collections where no catches occurred were omitted from consideration when analyzing model effects on Shannon's H' . Values of 0 were incorporated in analyses on bee abundance and species richness.

Bee species β -diversity across site disturbance type was analyzed using rarefaction curves (Colwell et al. 2012) produced by the 'iNEXT' package (Hsieh et al. 2020). Estimates were interpolated from sample-based abundances to account for different numbers of bee captures and extrapolated to 2x the size of the smallest sample (Chao et al. 2014), and multiple metrics were considered ($q = 0, 1,$ and 2). Bee community compositions were compared between disturbance types using a distance-based framework. Species-abundance matrices of bee captures from all sites (rows = sites, columns = bee species counts) were transformed into matrices of Bray-Curtis dissimilarities and effects of disturbance type were analyzed using the 'adonis2' function (per-mutational multivariate analysis of variance, n permutations = 9999) in the R add-on package 'vegan'.2.5-7 (Oksanen et al. 2019). Results

were visualized using non-metric multidimensional scaling (NMDS), produced with the 'metaMDS' function in package 'vegan'.

To compare relative effect size of forest structure and foraging habitat variables on bee assemblages, a generalized linear model framework (family: gaussian, link function: identity) was utilized, treating individual sites ($n = 39$) as the unit of analysis. Multi-year observations of floral resources and bee community metrics were averaged across the two years of collection to produce site-level averages (i.e., mean floral abundance and richness, mean bee abundance, richness, and diversity). Forest structural measurements (tree density, basal area, canopy cover) and woody debris measurements (fine and coarse woody debris surface loadings) did not differ between years and were treated as a single observation for each site. Independent variables used in the model were basal area, canopy cover (%), coarse woody debris surface fuel loadings (1000-hr fuels), fine woody debris surface fuel loadings (100-hr fuels), mean floral abundances, and mean floral richness. Tree density was omitted from analysis due to the variable's high correlation with basal area, whereas 1-hr and 10-hr fuel loadings were omitted due to high correlation with 100-hr fuel loadings. Dependent variables include mean bee abundance, bee species richness, and Shannon-Weiner diversity. Both independent and dependent variables were standardized to ($\mu = 0$, $\sigma = 1$) prior to analysis.

Results

Characterize the effects of disturbance type on forest structure and bee foraging habitat

Characteristics of overstory vegetation varied due to the effects of disturbance. Tree density differed significantly between disturbance types, with highest live tree densities in non-treated control stands (high severity = 32.1 trees per ha, low severity = 306.4 trees per ha, thinned = 321.2 trees per ha, non-treated control = 868.9 trees per ha; $F_{3,38} = 13.720$, $P = <0.001$; Fig. 2.2a); stand basal area was also significantly different between disturbance types with highest mean basal area in non-treated control stands (high severity = 0.028 m²/ha, low severity = 85 m²/ha, thinned = 109.2 m²/ha, non-treated control = 198.1 m²/ha; $F_{3,38} = 34.983$, $P = <0.001$; Fig. 2.2b). Canopy cover was significantly different across disturbance types, with the highest amount of cover found within non-treated control

sites (high severity = 0.4%, low severity = 36.8%, thinned = 38.1%, non-treated control = 63.9%; $F_{3,38} = 21.295$, $P = <0.001$; Fig. 2.2c).

In addition to stand structural attributes, elements of bee foraging habitat quantified throughout the growing season varied across disturbance types. Flora taxa typical of survey stands included *Achillea millifolium*, *Penstemon virens*, *Heterotheca villosa*, *Eriogonum umbellatum*, *Campanula rotundifolia*, *Sedum lanceolatum*, *Erigeron* spp., *Phacelia* spp., and *Solidago* spp. Mean floral abundance was 75.1%, 74.4%, and 50.4% higher in high severity burned stands than non-treated control, thinned, and low severity fire stands, respectively (whole model: $F_{3,73} = 5.683$, $P = 0.002$, Fig. 2.2d). Year-to-year variation had minimal effect on floral abundances and only accounted for ~2.2% of model variance. Similarly, average number of floral species was 77.6%, 56.3%, and 37.8% higher in high severity fire stands than in non-treated control, thinned, and low severity fire stands, respectively ($F_{3,73} = 9.924$, $P = <0.001$; Fig. 2.2e). Again, year-to-year variation had little effect on floral species richness and accounted for only 5.8% of modeled variance.

Bee nesting habitat also varied by disturbance type, with coarse woody debris surface loading 88.6%, 86.6%, and 49% higher in high severity fire stands than in non-treated control, thinned, and low severity fire stands, respectively ($F_{3,38} = 5.306$, $P = 0.004$; Fig. 2.2f). However, fined woody debris surface loading (i.e., 100-hr) did not differ significantly between disturbance types, though was 56.3%, 40.5%, and 6.6% higher in control stands than thinned, high severity, and low severity stands, respectively ($F_{3,38} = 0.728$, $P = 0.542$).

Subsequent linear regression analysis revealed a marginally positive association between 1000-fuel loading across disturbance types and floral abundance ($F_{1,38} = 4.428$, $P = 0.035$; Fig. 2.3a) and a significantly positive relationship with number of floral species ($F_{1,38} = 23.581$, $P = <0.001$; Fig. 2.3b), with 1000-hr fuel loading explaining a small proportion (~5-13 %) of variance in floral resources. Additional regression with the omission of outliers was performed in which we found no significant association between 1000-hr fuel loading and floral abundance ($F_{1,38} = 0.412$, $P = 0.525$; Fig. 2.3c), though a significant positive association between 1000-hr loading and number of floral species

persisted ($F_{1,38} = 5.528$, $P = 0.024$; Fig. 2.3d), with 1000-hr fuel explaining ~1-13% of variance in floral resources.

Quantify bee species abundance, richness and diversity among disturbance types

A total of 1,081 specimen were collected during the study. Overall bee γ -diversity was high and represented by 5 families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), 30 genera, and at least 70 species. Predominant genera consisted of bumblebees (*Bombus* spp.), mason bees (*Osmia* spp.), and digger bees (*Anthophora* spp.), accounting for 50.5%, 9.2%, 5.3 % of all collected bee specimens, respectively (Table 2.1). *Bombus appositus* Cresson was dominant within our sample, composing 14.4% of our total collected specimen. Other dominant species included across the sampling period include *Bombus centralis* Cresson (7.4% of total sample) and *Bombus bifarius* Cresson (7% of total sample).

Abundances of bees did not vary due to the main effect of disturbance type ($F_{3,227} = 1.8661$, $P = 0.136$), seasonality ($F_{2,227} = 0.471$; $P = 0.625$) or a disturbance type x seasonality interaction ($F_{6,227} = 0.933$, $P = 0.179$). However, on average the number of bees captured (abundance) was 18.45%, 23.99%, and 26.2% higher in high severity burned stands than in low severity burned, thinned, and non-treated control stands, respectively (Fig. 2.4a). Year effects accounted for 7.8% of the observed variation but this was not significant.

Bee species richness varied significantly due to the main effect of disturbance type ($F_{6,227} = 4.560$, $P = 0.004$). On average, number of bee species was higher in high severity stands than other disturbance types, with a 27.17%, 31.52%, and 40.76% difference between low severity, thinned, and non-treated control stands, respectively (Fig. 2.4b). However, there was no evidence that bee species richness was affected by seasonality ($F_{2,227} = 0.261$, $P = 0.771$) or a disturbance x seasonality interaction ($F_{6,227} = 1.310$, $P = 0.254$). Year effects were minimal and accounted for a small fraction (~0.6%) of variance in number of bee species.

Disturbance type also significantly affected bee α -diversity such that mean Shannon-Weiner diversity was 21.18%, 28.27%, and 31.73% higher in high severity burned stands than in low severity burned, thinned, and non-treated control stands, respectively ($F_{3,187} = 2.941$, $P = 0.034$; Fig. 2.4c). In

contrast, there was no evidence that diversity was affected by seasonality ($F_{2, 187} = 0.686, P = 0.505$) nor a disturbance type x seasonality interaction ($F_{6, 187} = 1.071, P = 0.382$). As with bee species richness, year-to-year effects were minimal and accounted for only ~0.5% of the variation in bee diversity.

When making specific contrasts between disturbance types, there was evidence that mean bee richness differed between low and high severity fire sites ($F_{1, 113} = 4.572, P = 0.035$); there were also marginally significant differences in mean bee abundance ($F_{1, 113} = 3.020, P = 0.085$) and α -diversity ($F_{1, 113} = 3.577, P = 0.062$; Fig. 2.5) between low and high severity burned stands. However, there was no evidence that mean bee abundance ($F_{1, 113} = 0.396, P = 0.530$), richness ($F_{1, 113} = 0.759, P = 0.386$), or diversity ($F_{1, 113} = 0.221, P = 0.640$) differed between thinned and non-treated control stands.

Analysis of β -diversity using rarefaction curves coupled with bootstrapped confidence intervals indicated that accumulation of bee biodiversity was generally higher in stands affected by high severity fire than in other disturbance types (Fig. 2.6). Additionally, species composition of bee community assemblages differed significantly between disturbance types ($F_{3, 38} = 1.362, P = 0.007$, Fig. 2.7a). Turnover ratios of two genera, *Bombus* and *Osmia*, primarily drove this difference, with the frequency of *Bombus* highest in non-treated control sites, and *Osmia* presence highest within low severity fire sites.

Compare relative effects of forest structure and foraging habitat on bee assemblages

Bee abundance was positively associated with increasing 1000-hr fuel loading ($\beta = 0.535, P = 0.036$) and with decreasing stand basal area ($\beta = -0.501, P = 0.037$; Fig. 2.8a, b). Mean bee species richness was marginally positively associated with 1000-hr fuel loading ($\beta = 0.400, P = 0.080$) and marginally negatively associated with increasing 100-hr fuel loading ($\beta = -0.279, P = 0.094$; Fig. 2.8c, d). Neither bee abundances nor mean bee species richness were significantly associated with modeled elements of foraging habitat. However, Shannon-Weiner diversity was positively associated with increasing floral abundance ($\beta = 0.342, P = 0.026$) and negatively associated with increasing stand basal area ($\beta = -0.468, P = 0.028$; Fig. 2.8e, f; Table 2.2).

Discussion

Our data shows that elements of bee foraging and nesting habitats in ponderosa-pine dominant dry mixed-conifer forests vary across a disturbance gradient, with consequences for bee community assemblages and ecosystem management efforts. Specifically, stands with high tree overstory mortality and low canopy cover following high severity wildfire had a greater abundance of floral species richness and abundance, and this was associated with increased bee richness and diversity. However, the same pattern was not true for stands that burned at low-severity or were treated by thinning—and these areas did not generally differ from non-treated stands in terms of bee abundance, richness, or diversity, although species compositions varied. Across all disturbance types, floral abundances and woody debris surface loadings were positively associated with bee diversity, whereas stand basal area and tree densities tended to be negatively associated with bee diversity. These results suggest that while disturbance types may differ in their specific effects on bee abundance or diversity, certain ecosystem structural variables also appear to have generalizable effects on bee assemblages. Accordingly, these variables (floral resources, woody debris loadings, and basal area and stand density) can be targeted by managers concerned with pollinator conservation.

The effects of wildfire burn severity as measured by tree mortality on bee assemblages were consistent with those described from previous studies, and our results coupled with previous findings provide growing evidence of a generally positive bee response to wildfire in the near-term. Overall, stands that were subjected to high severity fire experienced increases in bee species richness and diversity compared to low-severity, mechanically thinned, or non-treated stands. High fire severity sites were associated with reduction in stand basal area and reduced canopy cover, which can improve light availability in the understory (Nyoka et al. 2010). This increased penetration of sunlight to the forest floor promotes growth of forb species that provide foraging resources for native bees (Eltz et al. 2002; Jha and Vandermeer 2010), suggesting that disturbance resulting in canopy mortality may have cascading effects on bee site occupancy mediated via effects on floral resources. However, the effects of fire on bee communities are inconsistent, with some findings that indicate increasing fire severity promotes bee site occupancy (Potts et al. 2003; Galbraith et al. 2019a) and other studies that report

limited changes in bee communities or populations following fire (Lazarina et al. 2017; Simmons and Bossart 2020).

These conflicting results are likely because of differences in methodology when determining stand fire severity, inclusion of disparate time-since-fire treatments, differences in the indirect effects of plant species response to fire, direct effects of fire on bees (i.e. mortality), and the limited consideration of spatial heterogeneity of fire events, leading to variable estimations of fire impacts (Galbraith et al. 2019a) on bee communities. Conversely, bee community responses to fire likely differ across forest cover types or ecogeographic regions; example comparative studies have occurred in Mediterranean pine-scrublands (Lazarina et al. 2017), subtropical longleaf pine woodlands (Simmons and Bossart 2020), and Aleppo pine (*Pinus halepensis*) forests in Israel (Potts et al. 2003), providing evidence of bee response to fire disturbance at generally smaller spatial scales (Potts et al. 2003; Lazarina et al. 2017) or under the context of managed fire (Campbell et al. 2007; Rodríguez and Kouki 2015; Simmons and Bossart 2020). Exceptions to this include studies that have examined the influence of fire severity on bees in mixed-conifer forests of the Pacific Northwest (Galbraith et al. 2019a) and the effect of pyrodiversity on pollinators within forest-scrubland habitat of the western U.S. (Ponisio et al. 2016). Our study stands as one of the first to examine the effects of multiple fire severities and disturbance types on native bee communities within ponderosa pine forests.

Our results illustrate that stands affected by high-severity fire impacts bee β -diversity and community composition; specifically, *Bombus* (bumblebees, Apidae), generalists in both foraging and nesting behavior, were the most abundant taxa found across all disturbance types, comprising 50.5% of captures. The single most abundant species was *B. appositus* Cresson (white-shouldered bumblebee) which comprised 14.4% of the total collection and was found most frequently in thinned stands. However, other rare species including *B. californicus* Smith (California bumblebee), *B. fervidus* Fabricius (golden northern bumblebee), *B. fraternus* S. (Southern Plains bumblebee), *B. morrisoni* Cresson (Morrison bumblebee), and *B. occidentalis* Greene (western bumblebee) were identified in our surveys and were only captured in specific disturbance types (Table.2.3). *Osmia* (mason bees, Megachilidae) were also an abundant genus and represented ~9.2% of total bee captures, though

were greatest in high and low severity wildfire sites, composing 10.5% and 13.2% of captures in these treatments, respectively. This is consistent with the life history of *Osmia* as many species rely on woody debris for nesting habitat and high severity wildfire sites in particular experienced higher coarse woody debris surface loadings (Fig. 2.2f). Other taxa also varied across disturbance type: *Ceratina* spp. and *Augochlorella* spp. were found only in fire disturbed sites. More specifically, *Ashmeadiella* sp. and *Heriades* spp. were only found in sites that experienced high severity fire, while *Xeromelecta* sp. were found solely in low severity fire stands. In contrast, *Colletes* sp. and *Chelostoma* spp. were captured only in thinned stands, whereas *Duforea* sp. and *Coelioxys* sp. were found only in non-treated stands. Other taxonomic groups were habitat generalists and were found in all disturbance types including: *Agapostemon*, *Andrena*, *Anthophora*, *Diadasia*, *Halictus*, *Hoplitis*, *Lasioglossum*, *Lithurgopsis*, *Megachile*, and *Melissodes* (Fig. 2.7a). Thus, pyrodiversity and the resulting mosaic of forest structures remaining on the landscape following disturbance may promote landscape-level bee biodiversity (Kelly and Brotons 2017; Ponisio et al. 2016).

In contrast to effects of high-severity wildfire, forest thinning treatments did not influence bee populations relative to low-severity wildfire or non-treated stands. This differs from a recent study conducted in longleaf pine-savanna systems, which found that reduction of canopy cover through forest thinning resulted in increased bee species richness (Odanaka et al. 2020). Comparatively, another study conducted within northern hardwood forests provided evidence that small-scale removal of trees was attributed to increases in bee abundance, species richness, and diversity (Romey et al. 2007). In our study, thinning efforts were conducted with the intent of forest hazard reduction, whereas other studies include thinning treatments implemented to achieve commercial logging or restoration goals. Differences in forest thinning operations may result in varying stand structure with potentially different effects on associated insect communities, causing differences in observed bee response. Following thinning treatments, changes in important habitat resources such as woody debris and bare ground availability may disproportionately impact bees with specific life history traits. For example, bees in the genera *Megachile* and *Osmia* are known cavity nesters (Danforth et al. 2019) and may benefit from either the increased availability of woody surface debris left following treatment

(Peterson et al. 2005), or lack of change thereof. However, ground-nesting bees such as those in genus *Andrena* or *Lasioglossum* require bare ground for nesting (Danforth et al. 2019), which can be facilitated through the removal of trees and woody surface debris. Additionally, in some systems reduced tree density and associated canopy cover through thinning can be associated with increases in both plant abundance and diversity (Harrington and Edwards 1999; Nyoka et al. 2010), which could suggest more available habitat for insect pollinators in general. Although we did not find evidence for strong effects of thinning operations on regional bee assemblages, they can be interpreted to indicate that these forest management efforts are not likely to harm bee communities.

Habitat heterogeneity and complexity can benefit bees with varying life history strategies by diversifying nesting substrates (Potts et al. 2006) and availability of nesting sites. We found that coarse woody debris is associated with increased bee abundance and marginally increased bee species richness. As above, some genera of solitary bees, such as *Apidae*, *Megachile*, and *Osmia*, exploit debris such as fallen logs, beetle boreholes and galleries, and snags for nesting sites (Danforth et al. 2019). These components of bee habitat are often removed or altered as a result of disturbance events, including forest management practices, which may consider retention of surface debris (i.e., fuels) as undesirable (Peterson et al. 2005; Addington et al. 2018). However, there remains little known about how woody resources impact native bee populations, and this study is among the first to describe a positive relationship. Previous work reports variable results; some authors report that woody debris from salvage logging is associated with reduced bee species diversity (Galbraith et al. 2019b) whereas others report no association between woody debris and abundances of wood-cavity-nesting bees (Simanonok and Burkle 2019). Here, woody debris was correlated with decreased floral abundance but increased floral species richness, suggesting potential plant-mediated effects on bees in addition to provisioning of additional nesting sites. High surface fuel loadings (as well as high stand density or basal area) likely suppress understory production by reducing overall forb growing space, implying there may be surface loading thresholds that could facilitate both forb growth and bee nesting habitat. These relationships can potentially be exploited by land managers to conserve bee biodiversity. For example, application of our regression models suggests that a reduction in surface

fuel loadings from 15 to 25 Mg/ha is likely to be associated with a ~19% decline in bee species richness (Fig. 2.8e).

Several limitations of the present study should be considered when interpreting our results. First, abiotic variables that may contribute to study site variability were not measured but may impact bee sampling. Physical conditions such as mean site temperature, windspeed, and humidity are likely to impact both plant phenology and insect behavior (Fucini et al. 2014) at the microsite level and could provide additional insight on drivers of bee site occupancy. These effects merit further testing in ponderosa pine forests, for which there are few studies relating environmental conditions to bee communities or pollination services. Second, our study design does not incorporate landscape factors known to drive distributions of insect populations at large scales, including habitat connectivity, land cover richness, and proximity to heavily managed ecosystems such as agricultural lands or urban systems (Williams and Kremen 2007; Holzschuh et al. 2010). Inclusion of these factors in future analyses could supplement understanding of effects due to local vs. regional factors and will help to develop better models of bee species distributions. Lastly, our methodology utilizes blue vane traps, a passive sampling approach which can bias sampling towards certain taxonomic groups, especially bees with larger body sizes (such as bumblebees; Geroff et al. 2014; Gibbs et al. 2017). However, passive sampling with vane traps also offers the possibility of deploying sampling networks across large landscapes and over a short timeframe, which can reduce potential effects due to differences in species phenologies.

Our study is the first to comparatively assess effects of forest density reduction treatments and differential wildfire severity on native bee communities in a southwestern ponderosa pine forest ecosystem. Our findings contribute further evidence that pollinators benefit from disturbances in forested ecosystems, especially wildfire. We conclude that thinning treatments to reduce forest density and mitigate fire hazard and ignition risk did not negatively affect bee assemblages, and there was some evidence that thinning and burning disturbances are associated with different bee species compositions. A variety of habitat structures created by disturbance has variable effects on different bee functional groups and facilitates a wide range of resource availability that can cater to a variety of

exhibited life history traits. Land managers can target manipulation of tree stand density, woody debris, and floral resources for direct control of site-level bee assemblages but should also actively maintain a range of natural disturbances with the inclusion of pyrodiversity to conserve landscape-level bee biodiversity. Additional studies can elaborate on linkages between underlying mechanisms of bee response to forest disturbance to provide further understandings on cascading effects that can promote native bee conservation, particularly in a time of shifting climate and altered disturbance regimes.

Table 2.1. A summary of all bee specimens captured (γ -diversity) per disturbance type, arranged by taxonomic designation (genus-level).

Family	Genus	Disturbance type			
		control	high - severity	low - severity	thinned
Andrenidae	<i>Andrena</i>	2	2	3	2
Apidae	<i>Anthophora</i>	17	14	9	17
	<i>Apis</i>	1	2	7	2
	<i>Bombus</i>	137	169	136	104
	<i>Ceratina</i>	0	1	1	0
	<i>Diadasia</i>	6	3	2	9
	<i>Eucera</i>	2	1	1	2
	<i>Melecta</i>	1	4	0	1
	<i>Melissodes</i>	8	12	17	13
	<i>Svastra</i>	0	0	1	1
	Unknown	0	2	2	0
	<i>Xeromelecta</i>	0	0	1	0
	Colletidae	<i>Colletes</i>	0	0	0
<i>Hylaeus</i>		1	0	2	0
Halictidae	<i>Agapostemon</i>	3	4	1	7
	<i>Augochlorella</i>	0	1	1	0
	<i>Duforea</i>	1	0	0	0
	<i>Halictus</i>	6	21	9	12
	<i>Lasioglossum</i>	6	7	14	15
	<i>Sphecodes</i>	0	1	0	1
	Unknown	1	3	5	5
Megachilidae	<i>Anthidium</i>	0	0	1	1
	<i>Ashmeadiella</i>	0	1	0	0
	<i>Chelostoma</i>	0	0	0	2
	<i>Coelioxys</i>	1	0	0	0
	<i>Dianthidium</i>	1	1	2	6
	<i>Heriades</i>	0	3	0	0
	<i>Hoplitis</i>	8	14	7	9
	<i>Lithurgopsis</i>	6	6	4	4
	<i>Megachile</i>	20	16	3	15
	<i>Osmia</i>	14	34	35	16
	<i>Stelis</i>	0	0	1	1
Unknown	3	2	0	1	

Table 2.2. Summary of a generalized linear model to describe variation in bee assemblages due to effects of forest structure and foraging habitat. Significant ($P < 0.05$) and marginally significant ($P < 0.10$) effects are bolded.

Response variable	Parameter	Estimate (β)	SE	F	P
Bee abundance	Intercept	0.010	0.142	-	0.945
	Floral abundance	-0.047	0.167	0.06	0.780
	Floral species richness	-0.300	0.227	1.33	0.192
	Canopy cover	0.372	0.239	1.846	0.127
	Basal area	-0.501	0.233	3.532	0.037
	1000-hr fuels	0.535	0.248	3.56	0.036
	100-hr fuels	-0.082	0.181	0.156	0.652
Bee species richness	Intercept	0.004	0.128	-	0.975
	Floral abundance	0.131	0.151	0.571	0.390
	Floral species richness	-0.147	0.205	0.396	0.473
	Canopy cover	0.126	0.216	0.262	0.559
	Basal area	-0.331	0.21	1.894	0.121
	1000-hr fuels	0.400	0.224	2.444	0.080
	100-hr fuels	-0.279	0.164	2.227	0.094
Shannon's H'	Intercept	-0.005	0.126	-	0.965
	Floral abundance	0.342	0.148	4.054	0.026
	Floral species richness	-0.122	0.201	0.296	0.546
	Canopy cover	0.324	0.212	1.779	0.133
	Basal area	-0.468	0.207	3.924	0.028
	1000-hr fuels	0.265	0.22	1.112	0.232
	100-hr fuels	-0.184	0.161	0.649	0.359

Table 2.3. A summary of all *Bombus* specimens captured per disturbance type.

Genus	Species	Disturbance type			
		control	high severity	low severity	thinned
<i>Bombus</i>	<i>appositus</i>	40	44	15	57
	<i>auricomus</i>	0	0	0	1
	<i>bifarius</i>	33	19	15	9
	<i>californicus</i>	0	1	0	0
	<i>centralis</i>	38	15	19	8
	<i>fervidus</i>	0	3	0	9
	<i>flavifrons</i>	5	6	3	0
	<i>fraternus</i>	1	0	0	0
	<i>griseocollis</i>	1	1	1	3
	<i>huntii</i>	6	5	4	2
	<i>insularis</i>	3	4	4	2
	<i>melanopygus</i>	1	13	3	0
	<i>morrisoni</i>	0	0	0	1
	<i>nevadensis</i>	2	26	33	7
	<i>occidentalis</i>	2	1	0	0
	<i>rufocinctus</i>	3	26	37	5
	<i>sylvicola</i>	2	5	2	0

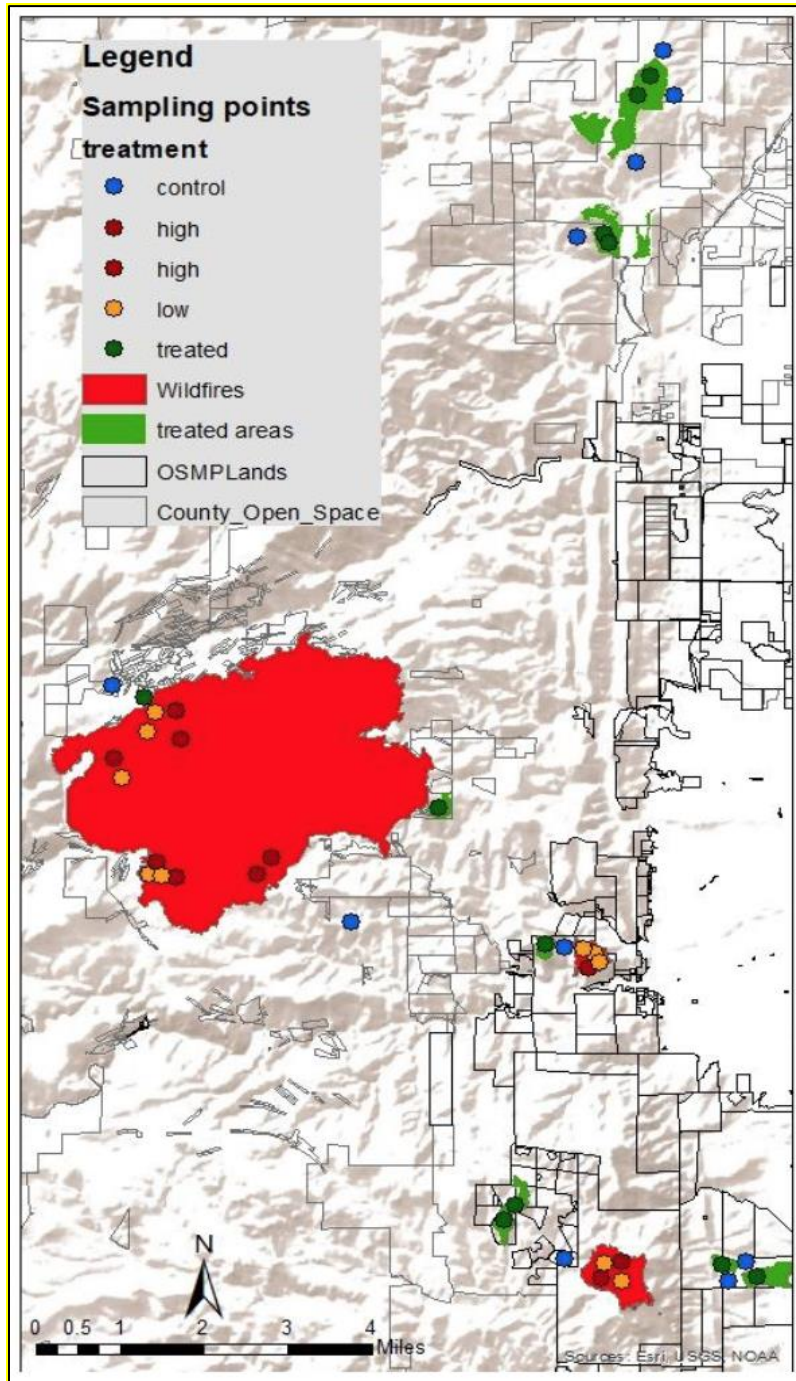


Figure 2.1. Map of study sites (Boulder County, CO) labeled (control plots indicated by blue, high severity plots in red, low severity plots in orange, thinned plots in green), wildfire burn scars (in red), and thinning treatment areas (in green).

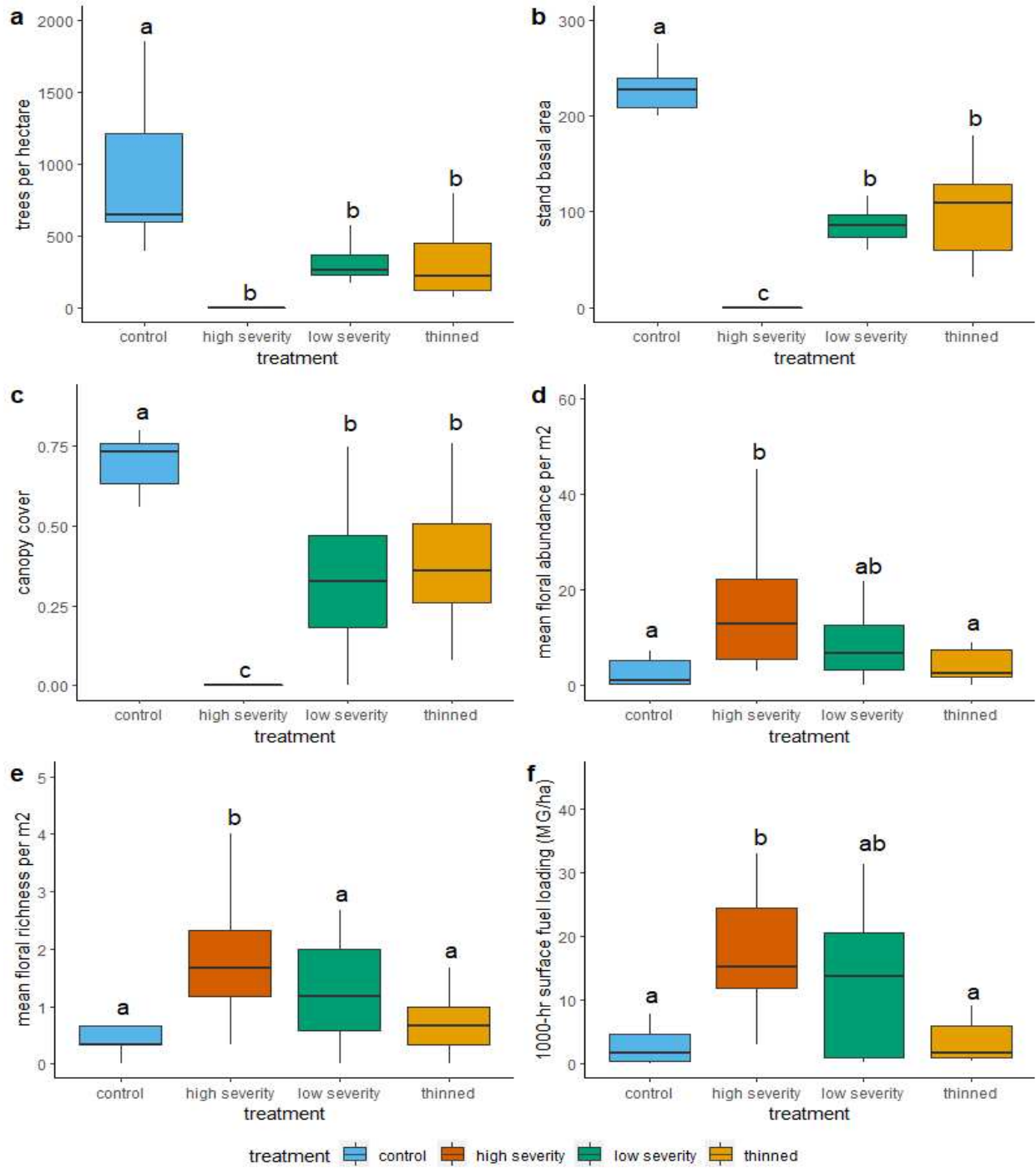


Figure 2.2. Distribution of stand structural attributes including (a) tree density, (b) stand basal area, and (c) canopy cover (%). Characteristics of foraging habitat including (d) floral abundances, (e) floral species richness, and (f) 1000-hr surface fuel loading were also quantified. Lettering denotes Tukey's HSD test.

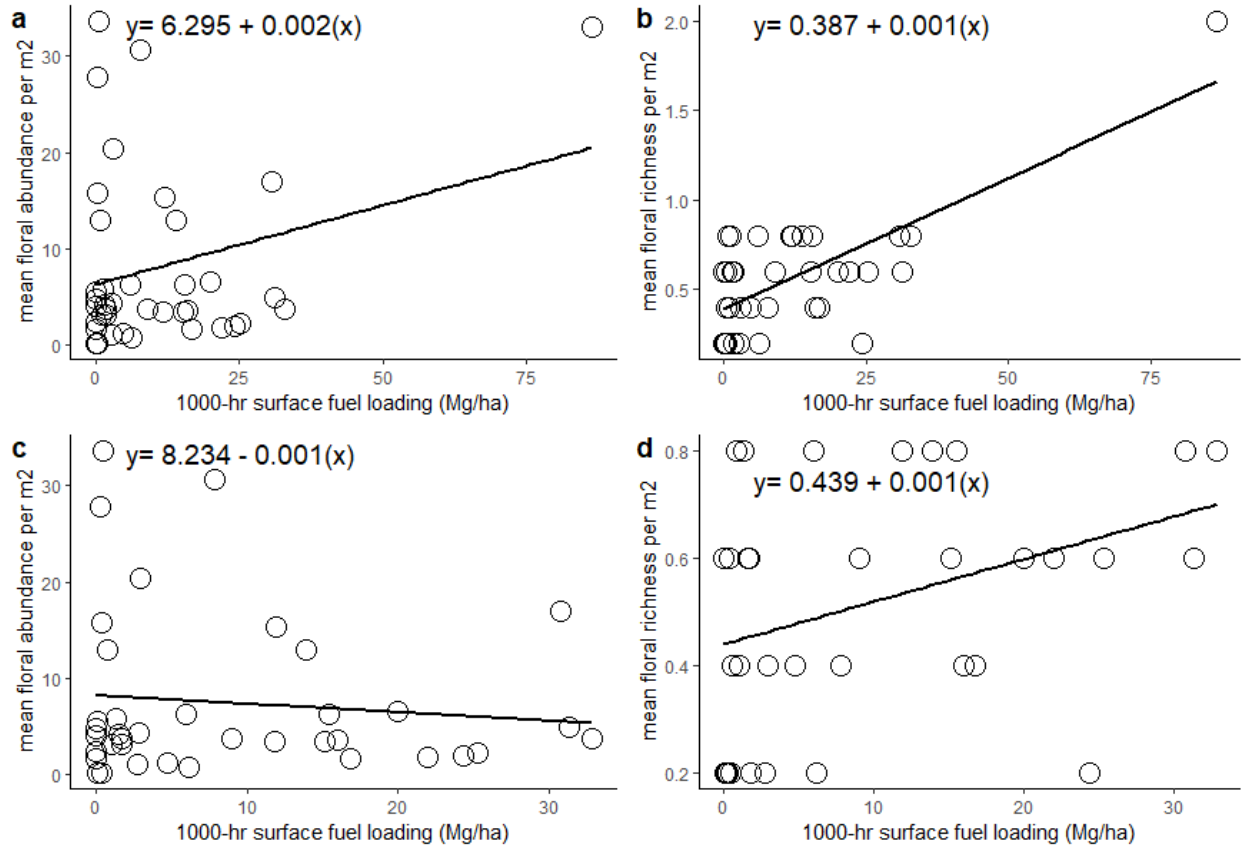


Figure 2.3. Relationship between 1000 hr fuel loading and (a) mean floral abundance, (b) mean floral species richness; Relationship between 1000 hr fuel loading and (c) mean floral abundance and (d) mean floral species richness with outlier plot removed. Both regression models are significant at a Type I error rate of $\alpha = 0.05$.

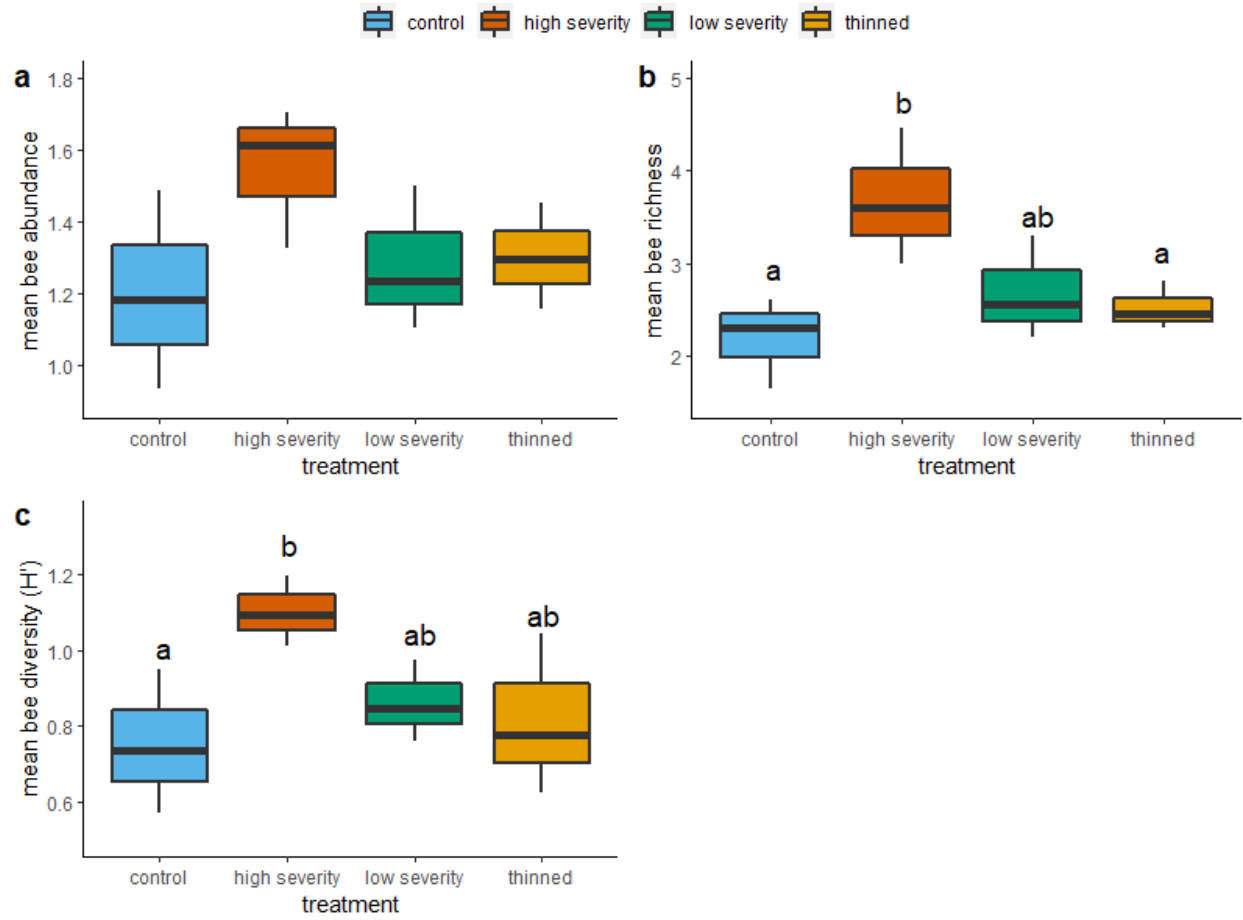


Figure 2.4. The distribution of (a) mean bee abundance, (b) mean bee richness, and (c) mean bee diversity (H') across disturbance type. Lettering indicates Tukey's HSD test, and boxplots not connected by the same letter in each panel are significantly different.

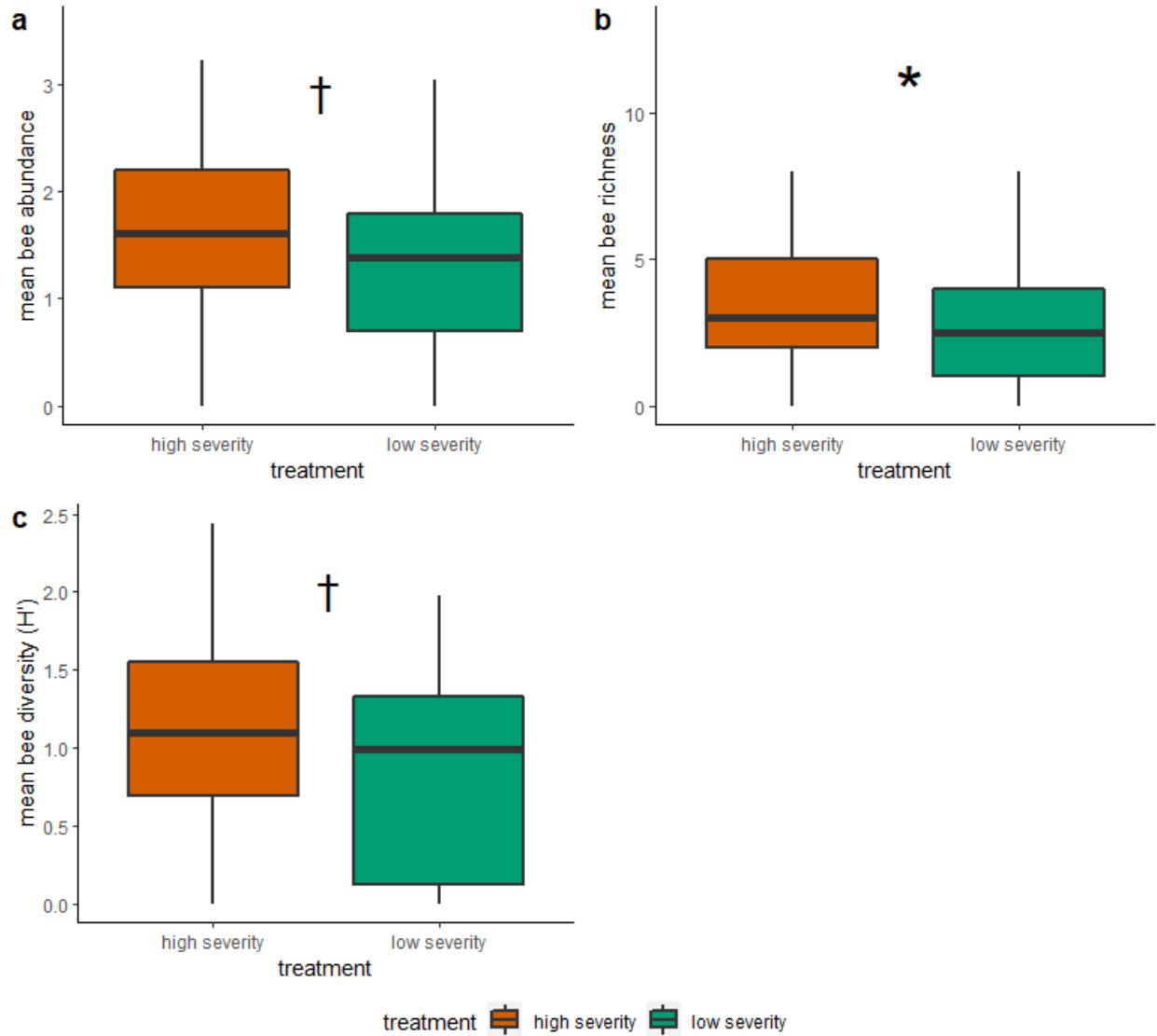


Figure 2.5. The distribution of (a) bee abundance, (b) richness, and (c) diversity compared between high and low severity fire stands. Asterisk denotes a significant difference ($P < 0.05$) between sample means, with the cross symbol signifying a marginally significant difference ($P < 0.10$).

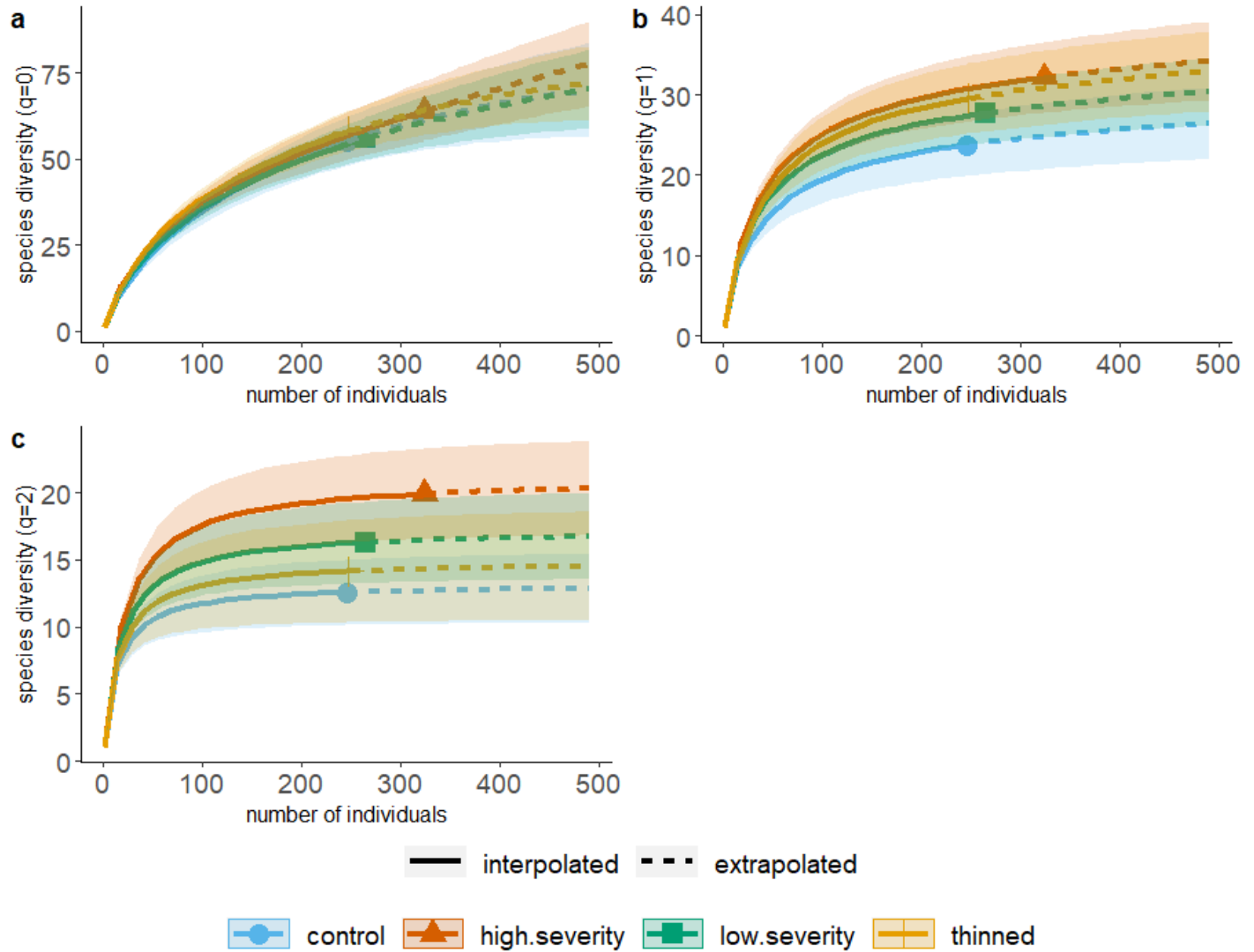


Figure 2.6. Sample-based accumulation of bee species diversity within disturbance types with Hill's numbers representing (a) species richness ($q = 0$), (b) Shannon's diversity ($q = 1$), and (c), Simpson diversity ($q = 2$). Shading represents the bootstrap-estimated 95% confidence interval for each sampling curve.

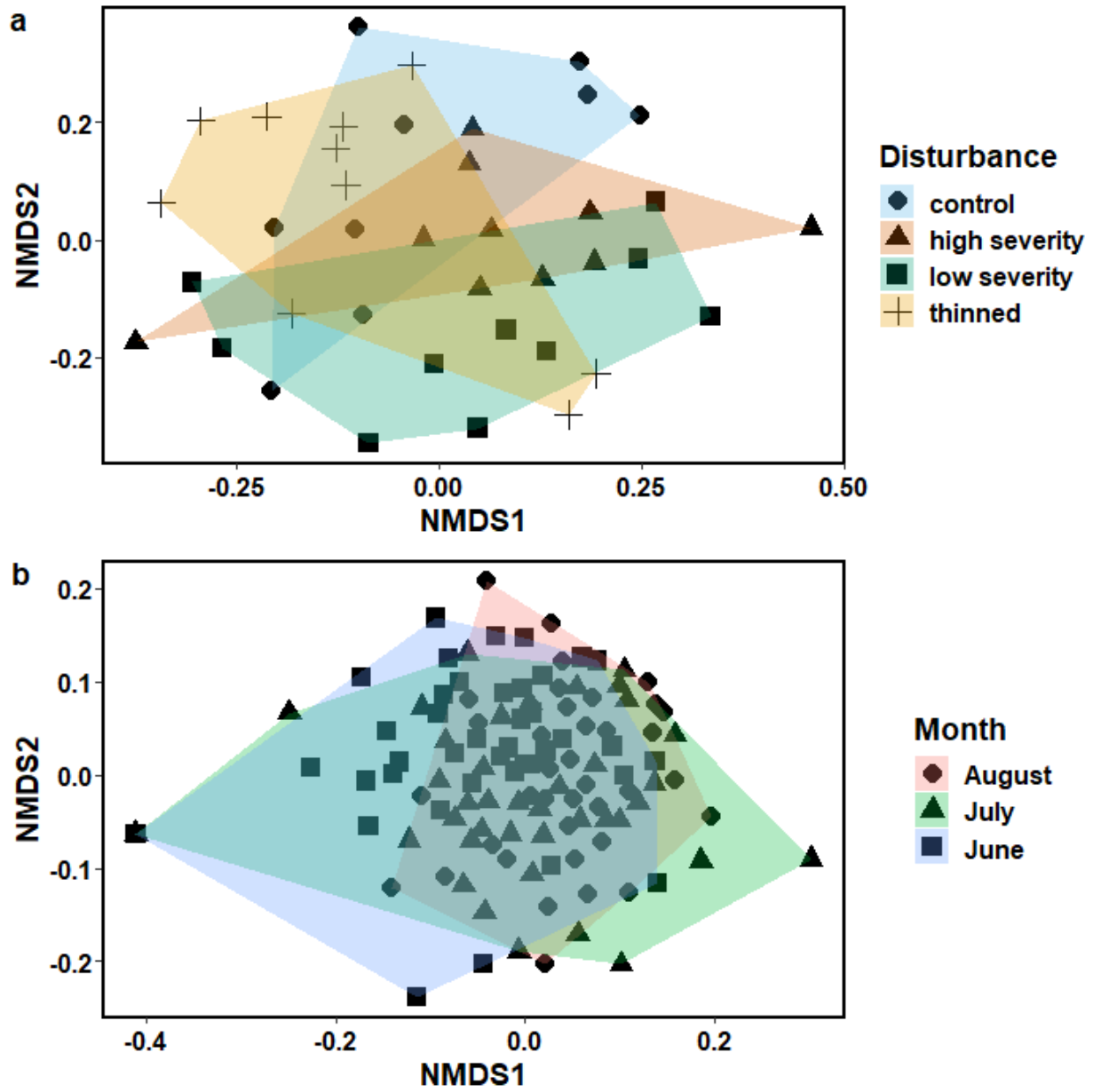


Figure 2.7. Ordination of bee community assemblages (NMDS), (a) compared between disturbance types and (b) sampling periods.

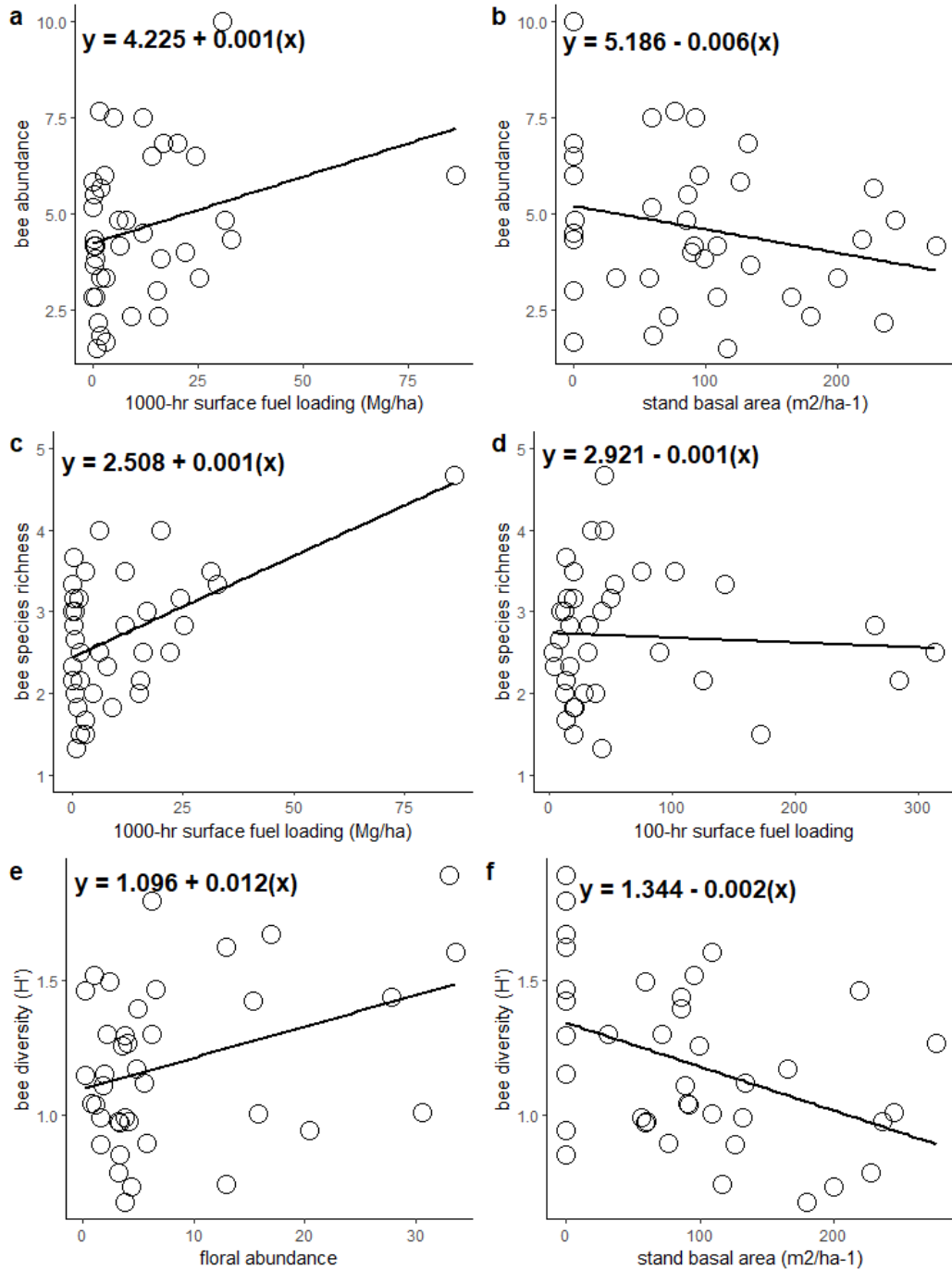


Figure 2.8. Relationship between bee abundance and (a) 1000-hr fuel surface loading and (b) stand basal area; bee species richness and (c) 1000-hr fuel surface loading and (d) 100-hr fuel surface loading; bee diversity and (e) floral abundance and (f) stand basal area. All regression models are significant at a Type I error rate of $\alpha = 0.10$.

CHAPTER 3: PRESCRIBED FIRE USE PROMOTES NATIVE BEE BIODIVERSITY IN A SEMI-ARID FOREST ECOSYSTEM

Overview

Insect pollinators, especially bees, are an essential component ecosystem function. Native bees provide key ecosystem services and shape the structure and composition of plant communities. However, recent research suggests a large-scale decline in bee populations, compelling the need for further research of the drivers and mechanisms influencing this decline. Within ponderosa pine ecosystems, fire suppression policies in the late 19th and early 20th century have led to the growth of dense stands with closed canopies and low understory production-this forest structure is widely considered undesirable for a variety of reasons. One approach to restoring the historic structure of these forests is to re-introduce fire disturbances to the landscape. Although the effects of managed or 'prescribed' fire on vegetation structure and composition are well-studied, relatively few studies have investigated whether prescribed fires have cascading effects on ecological communities important to ecosystem function, including native bees.

To address this knowledge gap, blue vane traps were used to sample native bee community assemblages across the growing season in ponderosa pine-forest sites in northern Colorado to evaluate the effects of prescribed fire restoration treatments, and time since treatment (1-yr post-fire, 3-yrs post-fire, non-treated controls), on bee populations. We quantified bee abundance, richness, and diversity as well as foraging resources (floral abundance and richness) and nesting habitat (coarse woody debris). From this, 5 key findings emerged: (1) Overall γ -diversity consisted of 5 families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), 25 genera, and at least 58 species. Predominant genera include bumblebees (*Bombus* sp.), mason bees (*Osmia* spp.), and digger bees (*Anthophora* spp.) which accounted for 61.4%, 13.9%, and 8% of collected specimens, respectively. (2) Pooled bee abundances varied across the season, with highest captures occurring early in the growing season; bee species richness and α -diversity varied across treatment type and

were highest within 1-year post-fire stands. (3) Unique bee community compositions were associated with different treatment types but also varied across the season. (4) Treatment type and seasonality were associated with differences in bee nesting habit. (5) Floral resource abundances and richness were associated with increased bee abundances, richness, and diversity, though stand basal area was negatively correlated with bee abundance and species richness.

Results here provide evidence that fire-disturbed forest stands generally promote bee site occupancy, but this effect is likely to peak shortly after fires and then decline. In addition, distinct bee assemblages were found in stands that were in varying states of time-since-fire, indicating that a mosaic of treatments likely support the greatest bee biodiversity at a landscape-scale. Further, findings here elucidate habitat structural components, specifically stand basal area and floral resource richness, that can be targeted by land managers to facilitate bee site occupancy. With this, we conclude the use of prescribed fire as a forest restoration method likely promote pollinator abundance and diversity in semi-arid ponderosa pine forests of the southwestern United States.

Introduction

Pollinators are critical components of healthy ecosystems where they provide pollination services to trees, shrubs, and herbaceous plants (Hanula et al. 2015). Within forested ecosystems, native pollinators are responsible for most pollination interactions (Hanula et al. 2016); for example, pollination of ~87% of wild plant species are directly dependent on insects (Ollerton et al. 2011), mainly native bees (Potts et al. 2010). Yet, despite their crucial role in ecosystem productivity - and evidence of their widespread decline (Gilgert and Vaughan 2011) - there is currently little known about factors regulating abundance or diversity of bee pollinators in Colorado or in forested systems in general (Koh et al. 2016). Forest management is widespread and utilized for a variety of goals, thus, it is likely that forest management methods impact pollination on large spatial scales.

Throughout much of the U.S. southwest region, ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) is a predominant forest cover type (Reynolds et al. 2013) that historically experienced frequent low- or mixed-severity fire events (Addington et al. 2018). These fires assisted in the maintenance of a heterogenous, open forest structure with large interspaces between trees within

stands. However, habitat conditions within southwestern pine forests have shifted as a result of past forest management (Covington and Moore 1994). In the late 19th and early 20th century widespread policies of fire exclusion, and extirpation of fire disturbances, resulted in high stem densities with closed canopies and low understory production in southwestern ponderosa pine systems (Allen et al. 2002). These uncharacteristically dense conditions pose as a threat to native bee populations by moving landscapes away from a mosaic forest structure and towards a homogenous forest structure (Nyoka 2010). High-density forest stands with closed canopies also reduces connectivity between habitat patches, hindering bee foraging or migration and potentially contributing to pollinator decline. For instance, closed canopy stands typically express reduced understory growth, leading to a lack of available food and nesting resources. Additionally, closed canopies prevent light from reaching the forest floor, reducing opportunity for thermoregulation; temperature and light are also important abiotic factors affecting bee foraging behaviors (Polatto et al. 2014). Consequently, the current 'non-historic' structure of regional southwestern ponderosa pine forests are likely to have various cascading effects on native bee populations, many of which could be deleterious. Despite these impacts, surprisingly few studies have examined how disturbances such as fire or restoration practices, including thinning and prescribed fire, impact bee communities.

In particular, prescribed fire is an important tool for natural resource stewards; restoring fire as a key ecosystem process can assist in reducing stand densities and maintaining desirable elements of ecosystem structure, function, and composition (Baker et al. 2007). Recent studies demonstrate that forest management and fire alter the structure of forest vegetation, but also site occupancy of forbaceous species (Laughlin and Fule 2008; Strahan et al. 2015; Kerns and Day 2018) - both factors are important to pollinator communities in forest ecosystems. Accordingly, it is probable that both fire and fire prevention strategies indirectly impact pollinator communities through effects on forest structure and forb abundance. The effects of prescribed fire on native bee communities remains relatively unexplored, indicating a need for research on interactions between fire disturbances, bee foraging and nesting habitats, and bee communities across a wide variety of forest cover types. Knowledge of these relationships is essential to better plan and implement forest management for the

conservation of bee biodiversity, and to describe the effects of forest restoration efforts on pollination services.

Here, we ask the question “How does prescribed fire impact a native bee assemblage in a forest system?”; We test the hypothesis that prescribed fire restoration treatments facilitate increases in abundance and species richness of native bees compared to non-treated forest stands. We sampled bee communities in areas that spanned multiple time-since-fire treatments to test: (a) how bee abundances, species richness, and diversity of bees vary with time-since-fire, and (b) how nesting and floral resources (i.e., tree density, stand basal area, canopy cover, coarse woody debris, floral species richness) may affect those relationships and differ among treatments. Our findings have implications for understanding how a widespread forest restoration tactic (i.e., implementation of prescribed fire) affects communities of native bees over time, with consequences for biodiversity and function of forest ecosystems.

Methods

Study system

Bees were collected from a total of 14 lower-montane sites in Red Feather Lakes, Colorado (40°51'17" N, 105°35'16" W; 2513 m elevation) during the growing seasons of 2018 using passive trapping methods. In the growing season of 2020, additional sites and treatments were included, for a total of 26 sites sampled at the conclusion of data collection (Fig. 3.1a, 3.1b). Overstory vegetation in stands selected from this study were predominantly ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), though lodgepole pine (*Pinus contorta* Douglas) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) reached the overstory in some areas. Sites were selected to represent three treatment types including sites that were (1) 1-year post-prescribed fire (n = 8), (2) 3-year post-prescribed fire (n = 9), and (3) non-treated control sites (n = 9).

Bee sampling procedure

Sites were sampled four times in each year of the study to capture seasonal variation in bee assemblages (Rhoades et al. 2018), including May, June, July, and August (N = 160 total bee sampling events). To sample bees, blue vane traps (Springstar, Inc. Woodinville, WA, USA) were hung during

each collection event from existing vegetation at a height of 1.3m for 48-h during periods of favorable weather at a density of one trap per site. Each trap included a wire mesh insert to provide refugia to trapped specimens in the case of unfavorable weather and three 1 mm drilled holes to reduce the probability of inundation with water. Upon the end of each sample period, traps were collected, and trapped specimens were euthanized by placing on dry ice. Specimens were then brought to the lab where all bees were pinned and identified to the lowest taxonomic level possible. In most cases this was genus to species, but some specimens could only be sorted to morphospecies. Voucher specimens are curated at the C.P. Gillette Museum of Arthropod Diversity at Colorado State University.

Forestry and understory measurements

At each collection location, site forest structural information was collected within a 0.01-ha fixed-area plot (10 m²). In each plot, trees were censused and their species identity as well as diameter at breast height (dbh) were recorded. Overstory canopy cover was recorded along two 8 m transects running north and south from plot center using a densitometer. The presence of both live and dead overstory cover above breast height was tallied. From these data basic forestry measurements were computed and used as variables for analysis, including stand basal area (m²/ha⁻¹), tree density (trees/ha⁻¹), and overstory canopy cover (%).

Site structural elements important to bee foraging and nesting were also measured. Coarse woody debris availability is an important predictor of potential nesting habitat, particularly for solitary bees (Rodriguez and Kouki 2015). To measure the availability of coarse woody debris (both sound and rotting material on the ground surface with proximal diameter >7.6cm), a 0.015-ha (6.9m radius) fixed-area plot around the trap location was utilized. Diameters of both ends of debris, as well as length, were recorded and included as a site-level estimate surface loading calculation in megagrams per hectare (MG/ha) (Brown et al. 1974).

In addition to nesting habitat created by woody debris, floral resource availability also directly influences bee site occupancy as a key foraging resource (Hanula et al. 2016). At each collection period, floral species richness was recorded using quadrats. At each site and collection period, five replicate 1m² quadrats were deployed and the total number of unique species represented by active

floral displays were recorded. One quadrat was placed directly beneath the trap location, with additional quadrats placed 2m in each cardinal direction. Quadrat measurements were treated as a subsample, and values from all five quadrats at each site were averaged together to yield a site-level mean floral abundance and richness for each collection period.

Data analyses

All statistical analyses were conducted using the R programming language (V3.5.2, "Eggshell Igloo"). A Type I error rate of $\alpha = 0.05$ was assigned for statistical significance to modeled effects.

A one-way ANOVA model was used to compare mean basal area, tree density, canopy cover (%), coarse woody debris surface loading, and floral richness due to the effects of prescribed fire (treatments = 1-yr post-fire, 3-yr post-fire, and non-treated control stands).

Two-way ANOVA was used to analyze the fixed effects of site treatment type (1-yr post-fire, 3-yr post-fire, and non-treated control), seasonality (May, June, July, August), and the treatment \times seasonality interaction on the responses of mean bee abundance, bee species richness, and bee α -diversity (as described by the Shannon-Weiner H' statistic); sample year was incorporated as a random effect (2018 or 2020). This analysis used site \times month \times year observations as the unit of replication ($N = 160$). Bee abundance data was log-transformed to conform to assumptions of normality prior to analysis. Shannon's H' cannot be calculated when no species are present ($H' = 0$ when a single species is present), therefore collections where no catches occurred were omitted from consideration when analyzing model effects on Shannon's H' (18.4% of observations); however, zeros were incorporated in analyses on bee abundance and species richness.

Bee β -diversity across treatments was analyzed using rarefaction curves (Colwell et al. 2012) produced by the 'iNEXT' package (Hsieh et al. 2020). Estimates were interpolated from sample-based abundances to account for different numbers of bee captures and extrapolated to approximately 2x the size of the largest sample (Chao et al. 2014), and multiple metrics were considered ($q = 0, 1,$ and 2). In addition to species accumulation rates, bee community compositions were compared between treatment types using a distance-based framework. Species-abundance matrices of bee captures from all sites (rows = sites, columns = bee species counts) were transformed into matrices of Bray-Curtis

dissimilarities and effects of treatment type were analyzed using the 'adonis2' function (permutational multivariate analysis of variance, n permutations = 9,999) in the R add-on package 'vegan' (Oksanen et al. 2019). Results were visualized using non-metric multidimensional scaling (NMDS). Additionally, chi-squared tests were used to assess whether the proportion of bee functional groups (as assigned by nesting behavior) varied by month of collection and treatment type. Nesting behaviors were divided into four categories based on exhibited life history strategies of each species: above ground nesters, below ground nesters, nesting generalists (above and below ground nesters), and parasitic species.

In addition to the effects of prescribed fire treatments, a generalized linear model framework (family: gaussian, link function: identity) was used to compare relative effect sizes of forest structure and foraging habitat variables on bee assemblages, treating unique site and treatment combinations ($n = 31$) as the unit of analysis. Bee community metrics were averaged across the two years of collection to produce site-level averages (i.e. mean bee abundance, richness, and diversity). Selected independent variables used in the model were stand basal area, tree density, canopy cover, woody debris surface loadings, and floral species richness. Tree density was omitted from analysis due to high correlation with basal area (Pearson's correlation coefficient $r = 0.821$). Response variables include mean bee abundance, bee species richness, and Shannon-Weiner diversity. Both independent and dependent variables were standardized to ($\mu = 0, \sigma = 1$) prior to analysis to simplify interpretation.

Results

How do bee abundance, species richness, and diversity of bees vary with time-since fire?

Characteristics of overstory vegetation between treatment types were similar. Tree density did not differ significantly between treatment types (1-yr post-prescribed burn = 129.3 trees per ha, 3-yr post-prescribed burn = 131.8 trees per ha, non-treated control = 158.3 trees per ha; $F_{2,30} = 0.476, P = 0.626$), nor did stand basal area (1-yr post-prescribed burn = 13.4 m²/ha, 3-yr post-prescribed burn = 12.6 m²/ha, non-treated control = 11.3 m²/ha; ; $F_{2,30} = 0.120, P = 0.887$) or canopy cover (1-yr post-prescribed burn = 30%, 3-yr post-prescribed burn = 26%, non-treated control = 37%; ; $F_{2,30} = 0.632, P = 0.539$).

Typical flora taxa identified during surveying include *Achillea millefolium*, *Cedum lanceolatum*, *Collinsia parviflora*, *Corydalis aurea*, *Geranium caespitosum*, *Penstemon virens*, *Phacelia* sp., *Potentilla fissa*, *Potentilla hippiana*, and *Solidago* spp. Mean floral richness was unaffected by a collection period × treatment interaction ($F_{3, 147} = 1.551$, $P = 0.166$), though across all treatment types floral richness was higher mid-growing season (June, July) than in other months of survey ($F_{3, 147} = 18.959$, $P < 0.001$; Fig. 3.2a). Mean floral richness was also highest in 1-year post-prescribed burn plots across all months of data collection with a 75.7% and 61.6% increase from non-treated control and 3-year post-prescribed burn plots, respectively ($F_{2, 147} = 6.360$, $P = 0.002$; Fig. 3.2b). Year-to-year- variation accounted for ~32% of modeled variance in floral richness but was not statistically significant ($P = 0.494$). Bee nesting habitat (coarse woody debris) did not differ significantly between treatment types ($F_{2, 30} = 2.349$; $P = 0.114$), though was 66.2% and 48.5% higher in non-treated control stands than in 1-year and 3-year post-burn plots, respectively.

A total of 1,096 bee specimens were collected across the two-year sampling period. Bee γ -diversity was represented by 5 families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), 25 genera, and at least 58 species. Predominant genera include bumblebees (*Bombus* sp.), mason bees (*Osmia* spp.), and digger bees (*Anthophora* spp.), accounting for 61.4%, 13.9%, and 8% of collected specimens, respectively (Table 3.1). Dominant species within our sample include *Bombus centralis* Cresson (18.7%), *Bombus bifarius* Cresson (9.7%), and *Bombus melanopygus* Nylander (7.9%).

Bee abundance significantly varied as result of seasonality ($F_{3, 147} = 12.686$, $P < 0.001$) and marginally varied due to the main effect of treatment type ($F_{2, 147} = 2.551$, $P = 0.082$). No significant variation in bee abundance was detected due to a treatment × seasonality interaction ($F_{6, 147} = 0.733$, $P = 0.624$). The average number of bee captures was 42.2% and 68.4% higher in 1-year post-fire stands than in non-treated control and 3-year post-fire stands, respectively (Fig. 3.3a). Further, bee abundances were highest early in the growing season (May), with 50.7%, 73.5% and 32.1% higher captures compared to that of June, July, and August, respectively (Fig. 3.4a). Year effects accounted for 29.7% of modeled variance in bee abundance but were not statistically significant ($P = 0.489$).

Bee richness varied significantly as a result of treatment ($F_{3, 147} = 5.497, P = 0.005$); however, bee species richness did not vary as a result of seasonality ($F_{3, 147} = 1.926, P = 0.128$) or a treatment \times seasonality interaction ($F_{6, 147} = 1.573, P = 0.159$). Bee richness was 37.6% and 61.1% higher in 1-year post-fire stands than in non-treated control and 3-year post-fire stands, respectively (Fig. 3.3b, 3.4b). Year effects account for 9.1% of modeled variance in bee richness but were not statistically significant ($P = 0.513$).

Bee α -diversity varied significantly as a result of treatment ($F_{3, 147} = 5.460, P = 0.005$), though diversity did not vary as a result of seasonality ($F_{3, 147} = 1.601, P = 0.192$) or a treatment \times seasonality interaction ($F_{6, 147} = 0.992, P = 0.434$). Shannon-Weiner diversity was 30.5% and 68.1% higher in 1-year post-fire stands than in non-treated control and 3-year post-fire stands, respectively (Fig. 3.3c, 3.4c). Year effects account for 26.2% of modeled variance in bee diversity, though this was not statistically significant ($P = 0.491$).

Analysis of β -diversity using rarefaction curves coupled with bootstrapped confidence intervals indicated that accumulation of bee biodiversity in 1-year post-fire stands exceeded that of recorded from other treatment types (Fig. 3.5), with bee biodiversity declining to below that of non-treated control stands by 3-years post prescribed fire. Additionally, species composition of bee community assemblages differed significantly across collection period ($F_{3, 92} = 3.069, P = 0.001$; Fig. 3.6a). Turnover ratios of *Bombus*, *Osmia*, *Anthophora*, and *Melissodes* primarily drove this difference, with *Bombus* captures highest in May, *Osmia* captures highest in June, and *Anthophora* and *Melissodes* most frequently encountered in August. Community assemblages also differed between treatment types ($F_{2, 28} = 1.327, P = 0.033$; Fig. 3.6b), with distinct turnover expressed by multiple genera of bees, including: *Diadasia*, *Nomada*, *Evylaeus*, *Sphecodes*, *Epeolus*, *Eucera*, and *Triepeolus* (Table 3.1).

Proportions of bee functional groups (as described by nesting habit) differed due to the effect of collection period ($X^2 = 76.317, P < 0.001$; Fig. 3.7a). Early-season (May) captures contained higher proportions of above ground nesting specialists, whereas late-season captures included higher proportions of nesting generalists. Proportions of bee functional groups represented in the sample also significantly differed between treatment types ($X^2 = 42.714, P < 0.001$) with higher ratios of

nesting generalists in 1-year post-fire stands, whereas 3-year post-fire stands experienced higher ratios of below ground nesting and parasitic species (Fig. 3.7b).

What are the relative effects of forest structure and foraging habitat on bee assemblages across the landscape?

Across all sampled stands, bee abundance was positively associated with increasing floral richness ($\beta = 0.564, P < 0.001$) and negatively associated with increasing stand basal area ($\beta = -0.472, P = 0.012$; Fig. 3.8a, b). Mean bee species richness was also positively associated with increasing floral species richness ($\beta = 0.670, P < 0.001$) and negatively associated with increasing stand basal area ($\beta = -0.406, P = 0.028$; Fig. 3.8c, d). Likewise, Shannon-Weiner diversity was associated with increasing floral species richness ($\beta = 0.670, P < 0.001$; Fig. 3.8e; Table 3.2).

Discussion

Our analyses demonstrate that low-intensity prescribed surface fires in southwestern ponderosa pine forests impact foraging resources (floral richness) important for native bees, and these effects cascade to impact bee assemblage α - and β -diversity. At 1-year post-fire, floral richness was enhanced in burned stands (Fig. 3.2b) and floral richness was positively correlated with bee abundance, richness, and diversity (Fig. 3.8). However, by 3-years post-fire this effect was diminished, and bee α -diversity was not different from non-treated control stands. This increase and then decline in diversity following prescribed fire was also associated with a shift in β -diversity, and bee assemblages were predominated by below-ground nesting specialists in 3-year post-fire habitats (Fig. 3.7). Collectively, these results suggest that prescribed fire use in southwestern ponderosa pine forests can have immediate positive effects on bee abundance and richness in forest stands and may also drive functional changes in bee communities over time.

In addition to prescribed fire effects, stands with lower basal area were associated with increased bee abundance and species richness. Reduction of stand basal area can increase penetration of sunlight to the forest floor, promoting growth of forb species necessary for successful bee foraging (Eltz et al. 2002; Jha and Vandermeer 2010; Rubene et al. 2015), increasing opportunity

for thermoregulation and further supporting foraging behavior as insects are most active in sunlit areas (Nyoka 2010).

Stands sampled 1-year post-fire exhibited increases in bee richness and diversity compared to stands that were 3-year post-fire and non-treated control stands. Stands that were 1-year post-fire also exhibited the highest mean floral richness, suggesting that prescribed fire use caused an increase in the availability of foraging resources for bees. Other studies have shown that prescribed fire can stimulate germination of existing seedbanks with heat or smoke (Read et al. 2000), which may explain the observed increase in floral richness. Moreover, bees often forage in early-seral habitats as these areas are typically have higher forb densities (Roberts et al. 2017), and as floral resource availability becomes consistent across the growing season a greater variety of foraging niche requirements are met (Bennett and Gratton 2013; Dorado and Vasquez 2014). Similar positive relationships between fire, floral richness, and bee diversity have been previously reported from other dry mixed-conifer forests of the western U.S., but have focused primarily on wildfire (Galbraith et al. 2019a; Burkle et al. 2019). In more mesic ecosystems, researchers have found evidence of fire promoting bee diversity at lesser years post-fire (Moylett et al. 2019), whereas in more arid systems floral and bee diversity may not peak until 2 years post-fire (Potts et al. 2003). There are also several key differences in the effects of prescribed fire and wildfire on forest structure that could have important consequences for the habitat resources that bees rely on. For example, prescribed fires are often managed to burn at low intensity and severity, whereas wildfires burn at variable intensities and may result in extensive areas tree mortality, leading to contrasting landscape characteristics. Additionally, prescribed fire is often administered in spring or fall, whereas wildfires often burn during summer months (Brown and Sieg 1996) with the potential for differential impacts on insect and plant communities.

There was evidence of distinct bee species turnover due to differences in time-since-fire treatments. *Bombus* (bumblebees, Apidae) were the most abundant taxa found across all treatment types, comprising 61% of total captures. The single most abundance species was *Bombus centralis* Cresson, a foraging generalist that comprised ~18% of the total collection and was found most abundantly within 1-year post-fire and non-treated control stands. Other species were only found in

specific habitats, including *B. fernaldae* Franklin (Fernald's cuckoo bumblebee, a parasitic species) and *B. fervidus* F. (golden northern bumblebee), which were captured in 3-year post-fire and non-treated control stands, respectively (Table 3.3). *Osmia* spp. (mason bees, Megachilidae) are generalist foragers and were relatively abundant in all habitats, though were most abundant in 1-year post-fire and non-treated control stands. In contrast, *Anthophora* spp. (digger bees, Megachilidae) were most abundant in 1-year and 3-year post-fire stands, indicating a potential preference for recently disturbed habitats. This is consistent with the life history of *Anthophora* as all species within the genus nest below ground and rely on bare soil substrate for suitable nesting sites (Wilson and Carril 2015; Youngsteadt 2020), which is likely increased in recently burned stands.

Bee community compositions also shifted significantly due to seasonal effects. The most abundant genera (*Bombus*, *Osmia*, and *Anthophora*) were captured in all months of collection. Though bee α -diversity was unaffected by seasonality, abundances of most genera varied across the collection period. Some taxa exhibited specific phenologies and were captured only at certain times in the growing season; for example, *Melecta* and *Sphecodes* were found early-season (May) whereas *Ashmeadiella*, *Colletes*, *Dianthidium*, *Epeolus*, *Eucera*, *Stelis*, and *Triepeolus* appeared late-season (July and August). Many of the genera exhibiting seasonal specificity are either specialist foragers or parasitic (Wilson and Carril 2015), and these groups may exhibit greater sensitivity to seasonal pulses in floral resources or host bee reproductive cycles.

Analyzing bee abundances by their nesting behaviors indicated evidence for functional variation in bee communities across the growing season and across treatment type. We observed higher numbers of nesting generalists in 1-year post-fire stands relative to other treatment types, whereas 3-year post-fire stands bees that specialize in below-ground nesting were more frequent. This pattern may be explainable due to physical effects of prescribed fire treatments: burning consumes woody debris and surface vegetation and increases bare soil cover (Allen et al. 2002; Nyoka 2010), altering habitat availability for cavity-nesting and ground-nesting bees, respectively. This matches with a recent study from southeastern forests, which showed that prescribed fire led to higher densities of ground-nesting bees (Ulyshen et al. 2021). However, we did not detect a positive response of ground-

nesting bee species to prescribed fire until 3 years post-fire, potentially indicating a delayed response of bee functional variation to fire disturbance in more arid forest systems.

This study has several limitations that should be considered when approaching future research design. Foremost, abiotic factors that may have contributed to site variability were not measured but have potential to impact bee sampling. Physical conditions including mean site temperature, humidity, and windspeed likely impact both plant phenology and insect behavior (Fucini et al. 2014) at the microsite level and provide additional insight on drivers of bee species distributions. Second, our study design does not include landscape factors known to drive distributions of insect populations at large scales, including land cover richness, habitat connectivity, and proximity to heavily managed ecosystems such as agricultural lands, urban systems, or other extensive land management operations. Inclusion of regional to landscape-level factors in future analyses could help develop improved models of bee species distributions that incorporate comparison of effects between small- and large-scale factors. Lastly, our collection method uses only single approach (vane traps), but inclusion of multiple collection methods (e.g., vane traps, colored pan traps, and aerial netting) reflects a broader representation of bee biodiversity overall (Rhoades et al. 2017).

This study is among the first to assess effects of prescribed fire treatment and associated time-since-fire effects on native bee communities in a southwestern ponderosa pine forest system. The analyses reported here contribute to a growing body of evidence that fire disturbance, including low intensity prescribed fire use, is associated with near-term benefits for forest bees. Different post-fire timesteps were associated with distinct bee community composition and functional variation. Further, land managers can manipulate stand basal area and floral resources to control site-level bee assemblages but are recommended to facilitate a heterogenous forest structure to promote landscape-level bee biodiversity. Future studies can explore connections between underlying mechanisms of bee response (e.g., floral resource characteristics, landscape-level factors, bee life history traits) to prescribed fire treatments to contribute further understanding on how to manage, or account, for native bee conservation in a time of widespread insect pollinator decline and a shifting climate.

Table 3.1. A summary of bee genera captured in this study and their abundances by treatment type (i.e., time-since-fire and non-treated control stands).

Family	Genus	Treatment		
		1-yr post-fire	3-yr post-fire	control
Andrenidae	<i>Andrena</i>	4	1	4
Apidae	<i>Anthophora</i>	51	15	22
	<i>Apis</i>	1	1	0
	<i>Bombus</i>	317	106	249
	<i>Diadasia</i>	1	0	0
	<i>Epeolus</i>	0	0	1
	<i>Eucera</i>	0	0	1
	<i>Melecta</i>	0	3	1
	<i>Melissodes</i>	10	4	14
	<i>Nomada</i>	1	0	0
	<i>Triepeolus</i>	0	1	0
	Colletidae	<i>Colletes</i>	0	1
<i>Hylaeus</i>		3	1	2
Halictidae	<i>Agapostemon</i>	3	0	1
	<i>Dialictus</i>	2	0	2
	<i>Evylaeus</i>	6	0	0
	<i>Halictus</i>	3	3	5
	<i>Lasioglossum</i>	30	10	7
	<i>Sphecodes</i>	3	0	0
	Unknown	1	0	0
Megachilidae	<i>Ashmeadiella</i>	1	0	2
	<i>Dianthidium</i>	4	0	4
	<i>Hoplitis</i>	10	4	5
	<i>Megachile</i>	9	2	5
	<i>Osmia</i>	91	7	54
	<i>Stelis</i>	1	2	0

Table 3.2. Summary of a generalized linear model analysis to describe variation in bee assemblages due to effects of forest structure and foraging habitat. Significant ($P < 0.05$) effects are bolded.

Response variable	Parameter	Estimate (β)	SE	F	P
Bee abundance	Intercept	-0.032	0.133	-	0.809
	Floral richness	0.564	0.140	13.307	< 0.001
	Canopy cover	0.313	0.159	3.168	0.057
	Basal area	-0.472	0.177	5.854	0.012
	Coarse woody debris	0.126	0.168	0.462	0.456
Bee richness	Intercept	0.001	0.134	-	0.994
	Floral richness	0.581	0.140	14.072	< 0.001
	Canopy cover	0.256	0.160	2.107	0.117
	Basal area	-0.407	0.177	4.329	0.028
	Coarse woody debris	0.209	0.168	1.262	0.221
Shannon-Weiner diversity	Intercept	-0.032	133	-	0.812

Table 3.3. A summary of all *Bombus* species captured per treatment type.

Genus	species	1-yr post-fire	3-yr post-fire	control
<i>Bombus</i>	<i>appositus</i>	33	8	21
	<i>bifarius</i>	23	55	28
	<i>californicus</i>	4	0	2
	<i>centralis</i>	87	20	98
	<i>fernaldae</i>	0	1	0
	<i>fervidus</i>	0	0	2
	<i>flavifrons</i>	38	0	32
	<i>griseocollis</i>	2	2	1
	<i>huntii</i>	11	0	3
	<i>insularis</i>	10	0	5
	<i>melanopygus</i>	59	0	27
	<i>nevadensis</i>	10	10	8
	<i>occidentalis</i>	1	1	0
	<i>rufocinctus</i>	20	7	9
	<i>sylvicola</i>	18	2	13
	sp. 1	1	0	0

RFX Unit 28

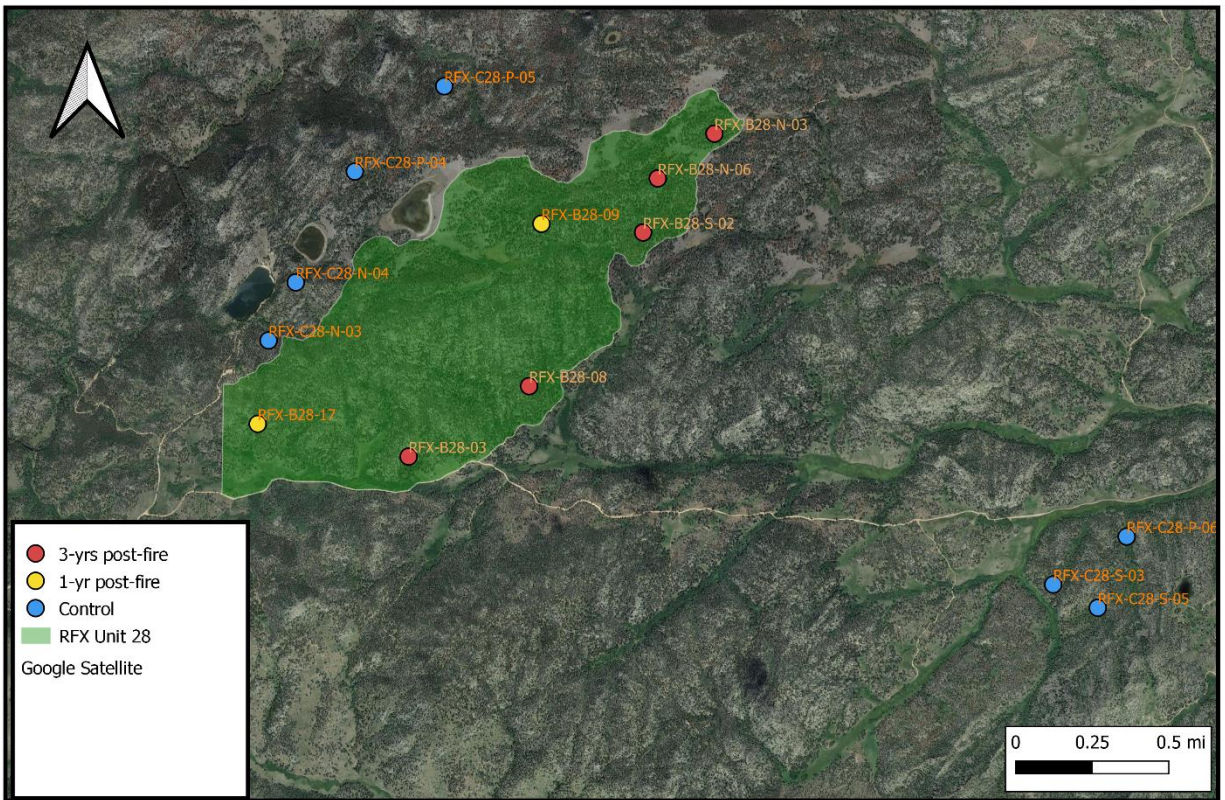


Figure 3.1a. Map of sites at Red Feather Lakes, CO with plots labeled and prescribed burn treatment area denoted (in green).

Elkhorn 4 RX Unit

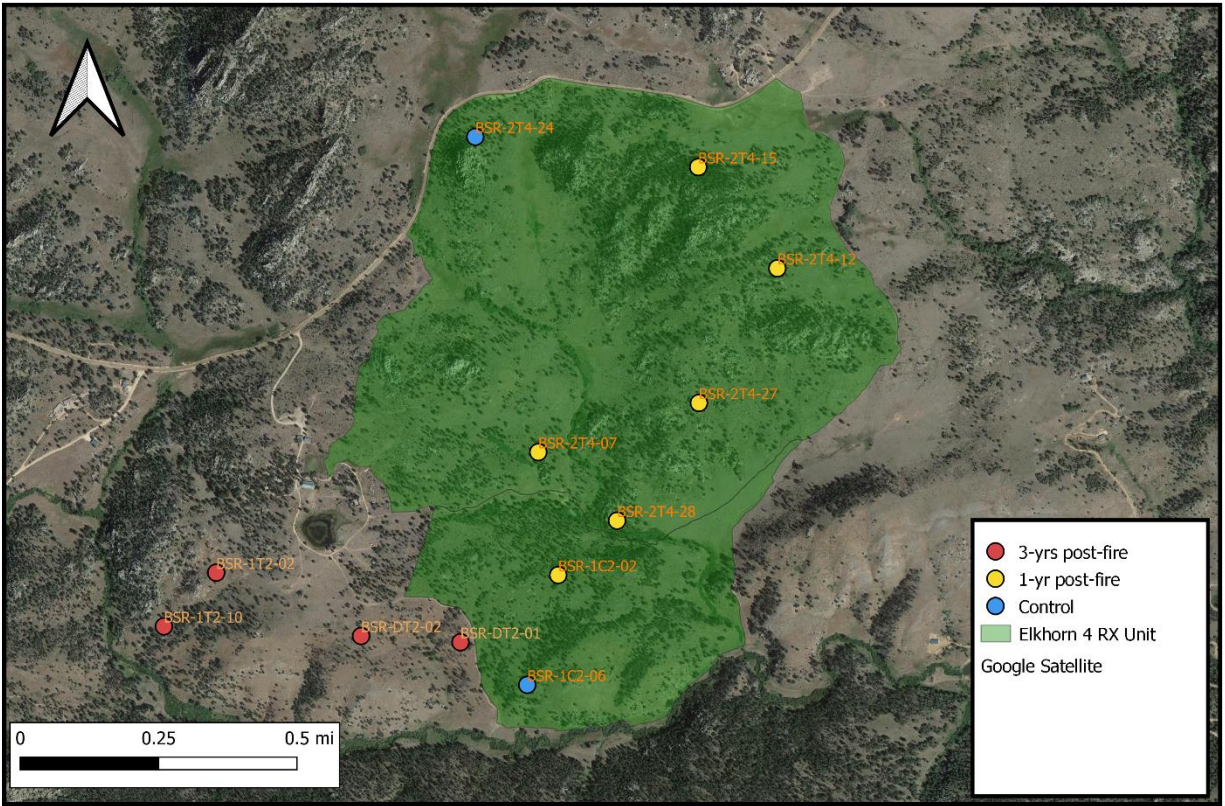


Figure 3.1b. Map of sites at Ben-Delattour Scout Ranch, CO with plots labeled and prescribed burn treatment area denoted (in green).

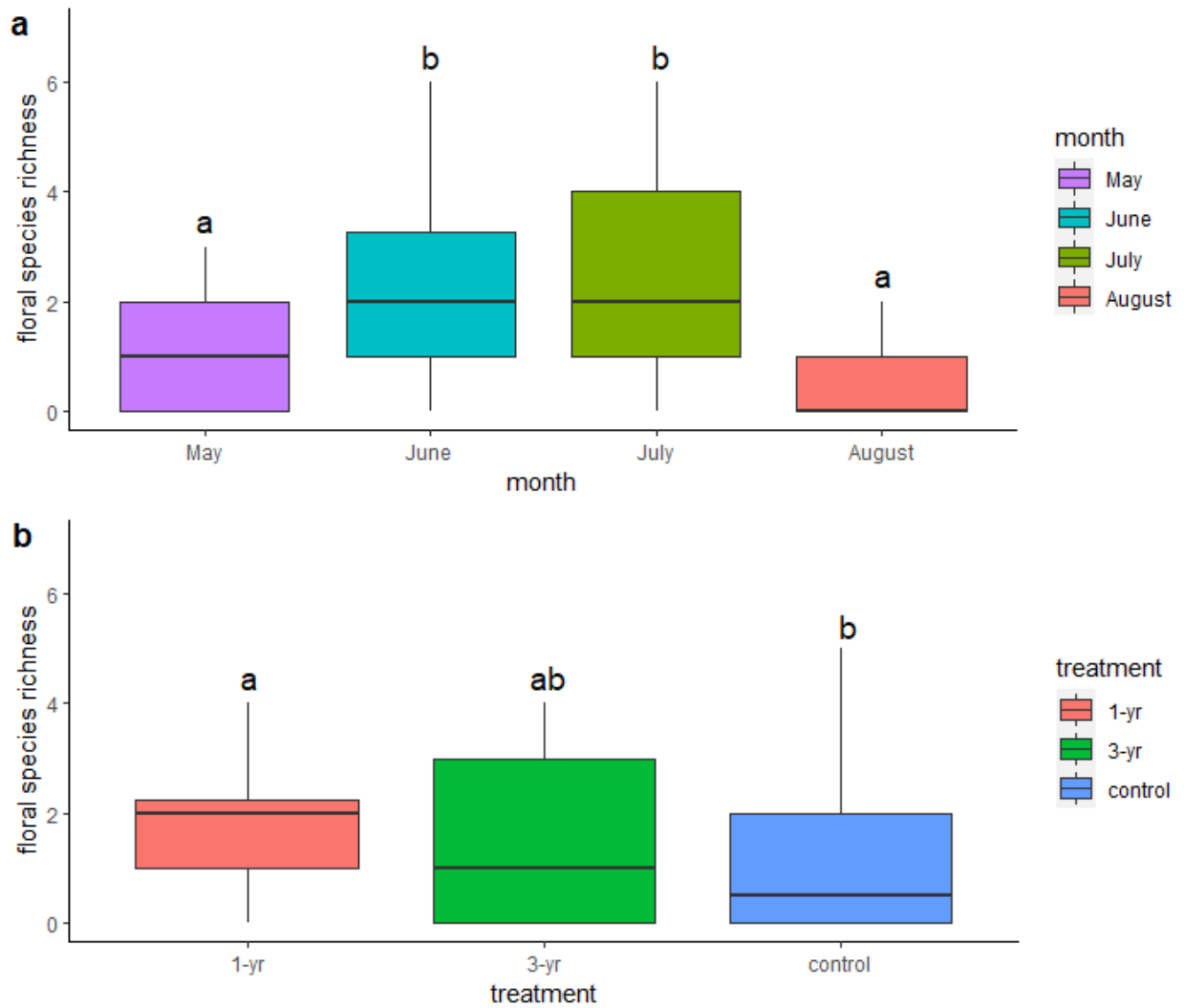


Figure 3.2. Distribution of bee foraging habitat across (a) collection period and (b) treatment type. Lettering denotes Tukey's HSD test; boxplots not connected by the same letter differ significantly in mean value.

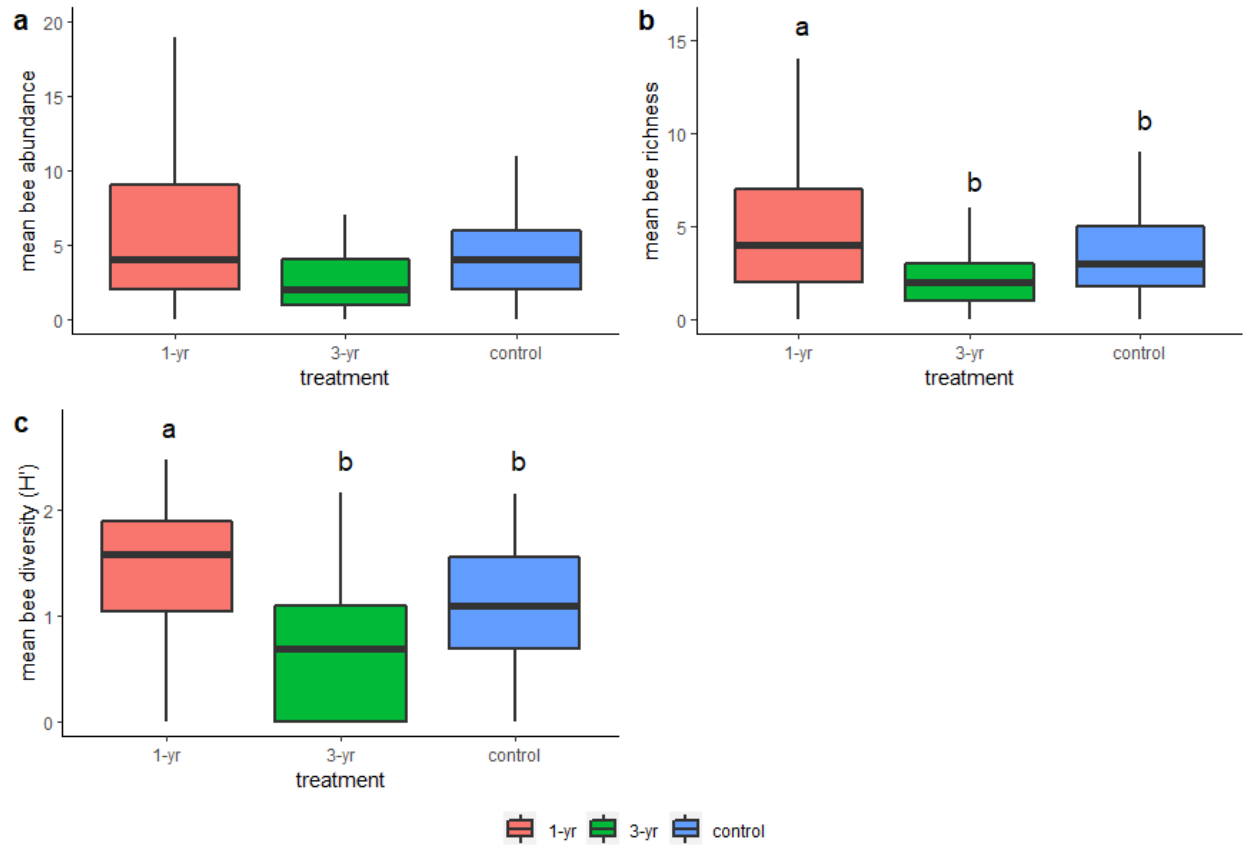


Figure 3.3. The distribution of (a) mean bee abundance, (b) mean bee richness, and (c) mean bee diversity (Shannon's H' statistic) due to the effects of prescribed fire treatment. Lettering indicates Tukey's HSD test, and boxplots not connected by the same letter in each panel are significantly different.

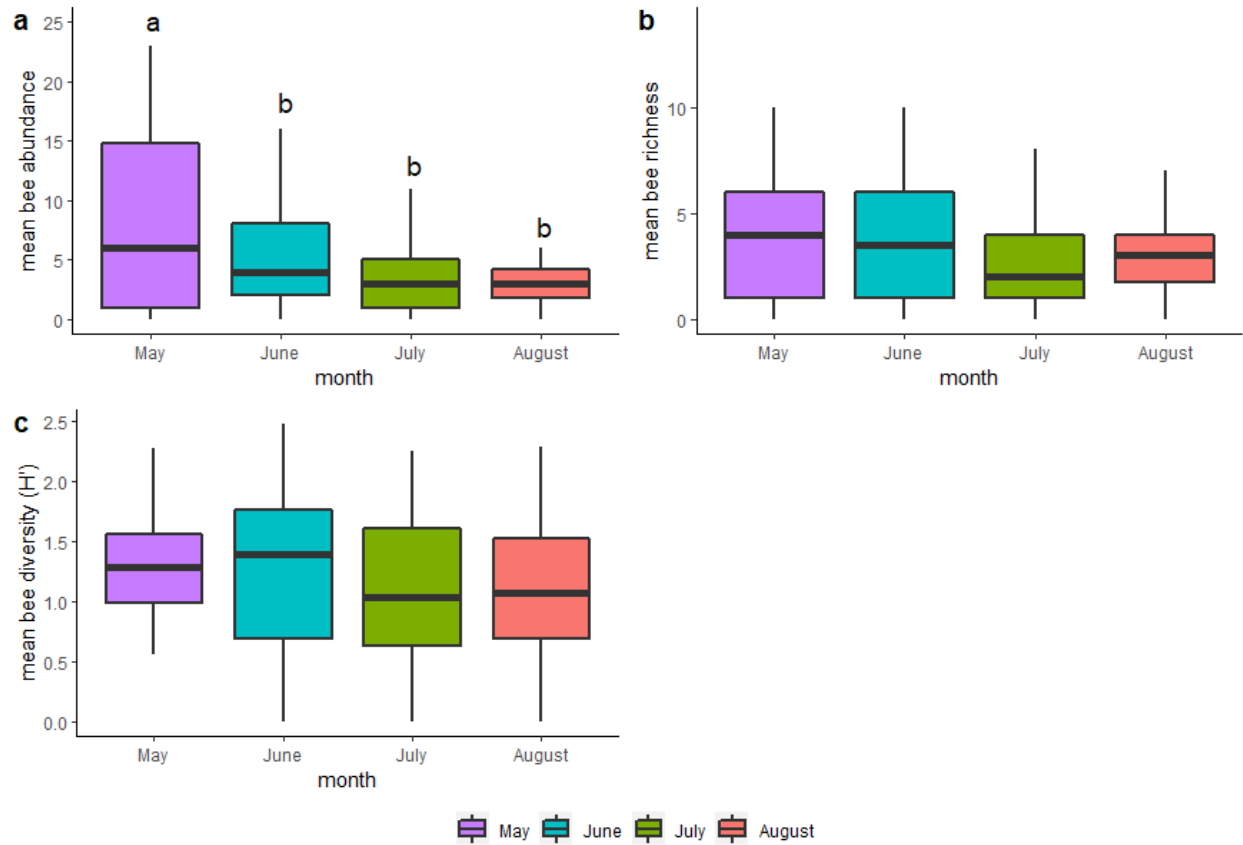


Figure 3.4. The distribution of (a) mean bee abundance, (b) mean bee richness, and (c) mean bee diversity (H') across collection period. Lettering indicates Tukey's HSD test, and boxplots not connected by the same letter in each panel are significantly different.

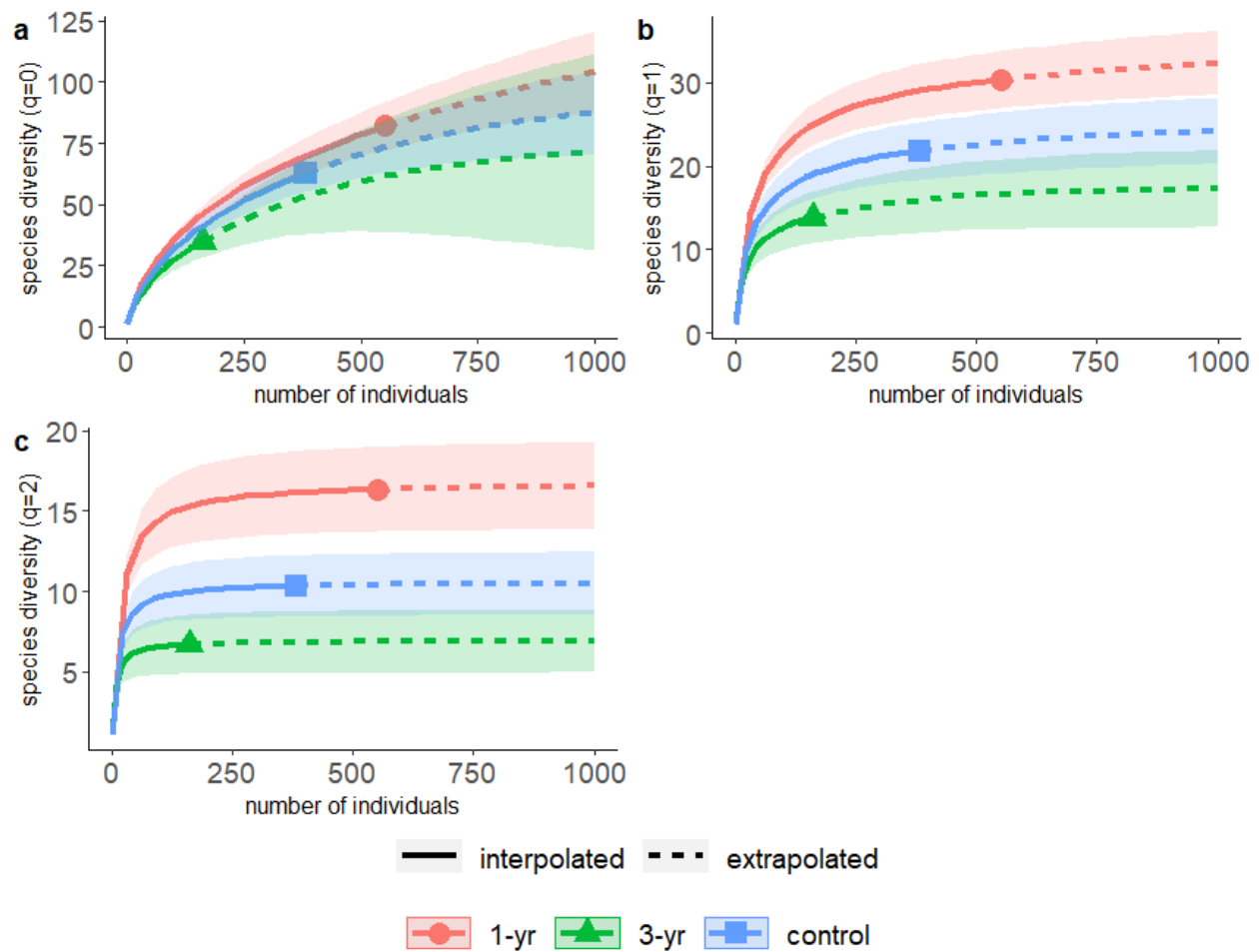


Figure 3.5. Sample-based accumulation of bee species diversity within treatment types with Hill's numbers representing (a) species richness ($q = 0$), (b) Shannon's diversity ($q = 1$), and (c), Simpson diversity ($q = 2$). Shading represents the bootstrap-estimated 95% confidence interval for each sampling curve.

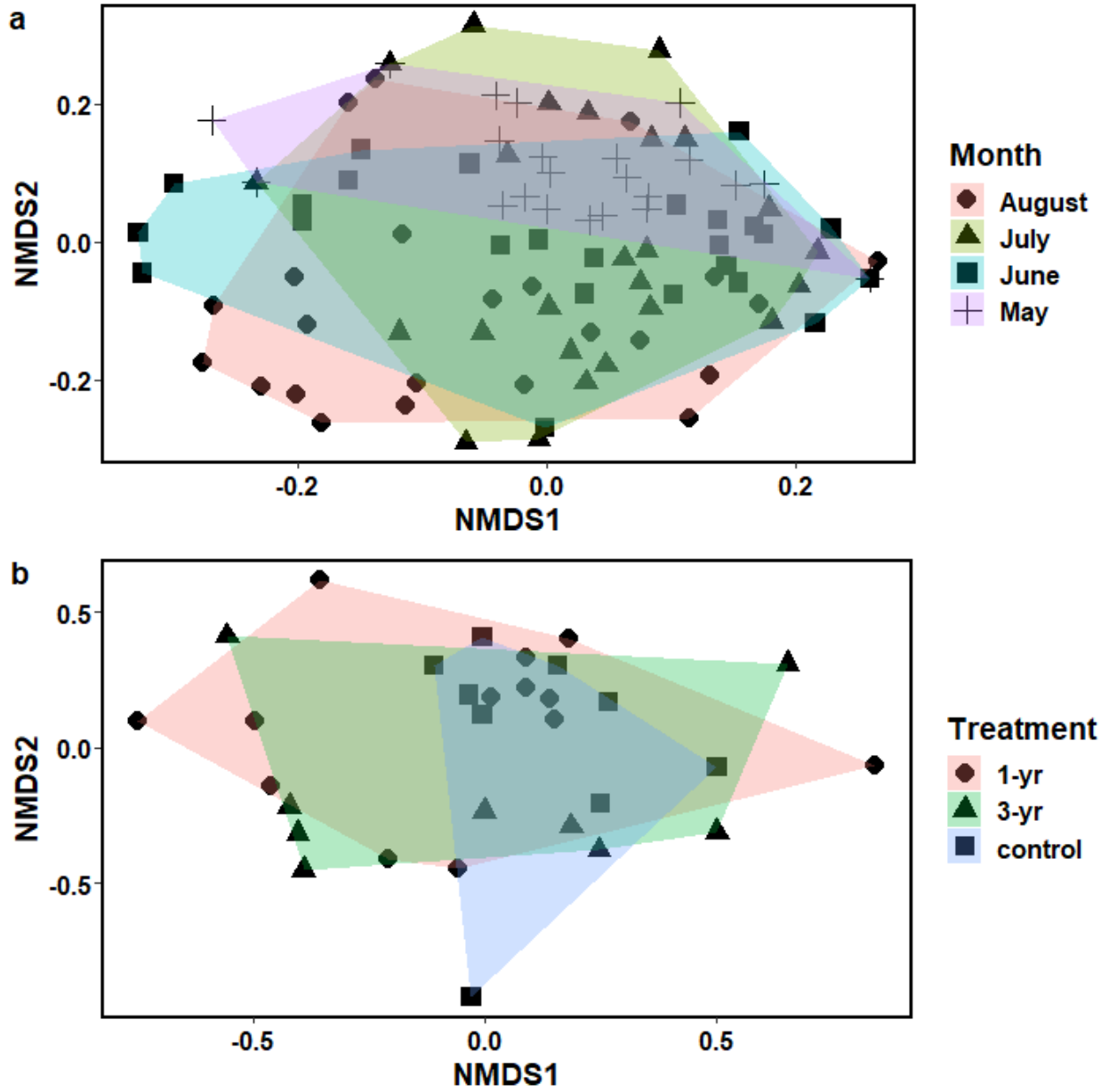


Figure 3.6. Ordination of bee community assemblages (non-metric multi-dimensional scaling) across (a) collection period and (b) treatment type.

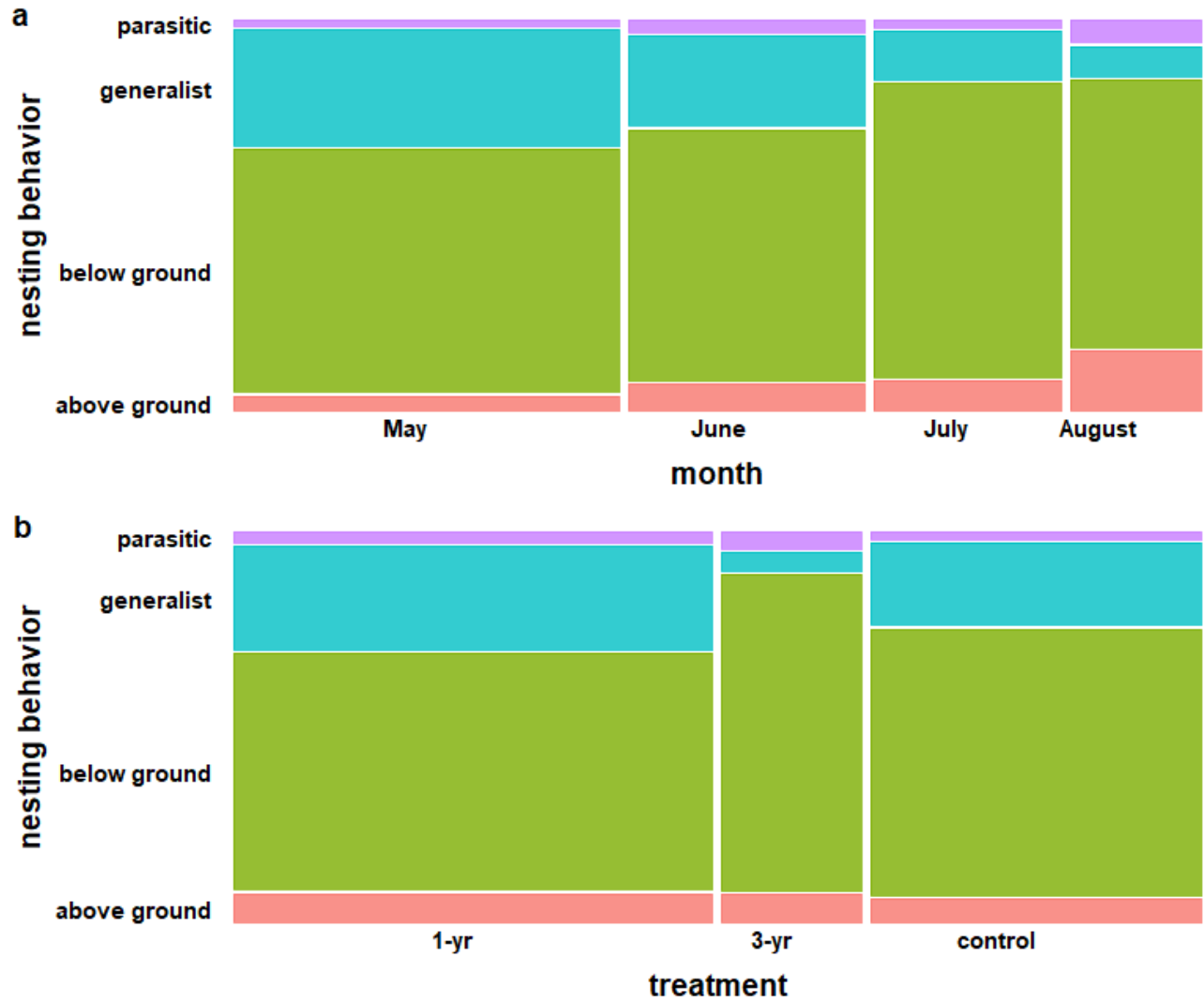


Figure 3.7. Mosaic plot illustrating ratios of observed nesting behavior among captured bees within each (a) collection period and (b) treatment type.

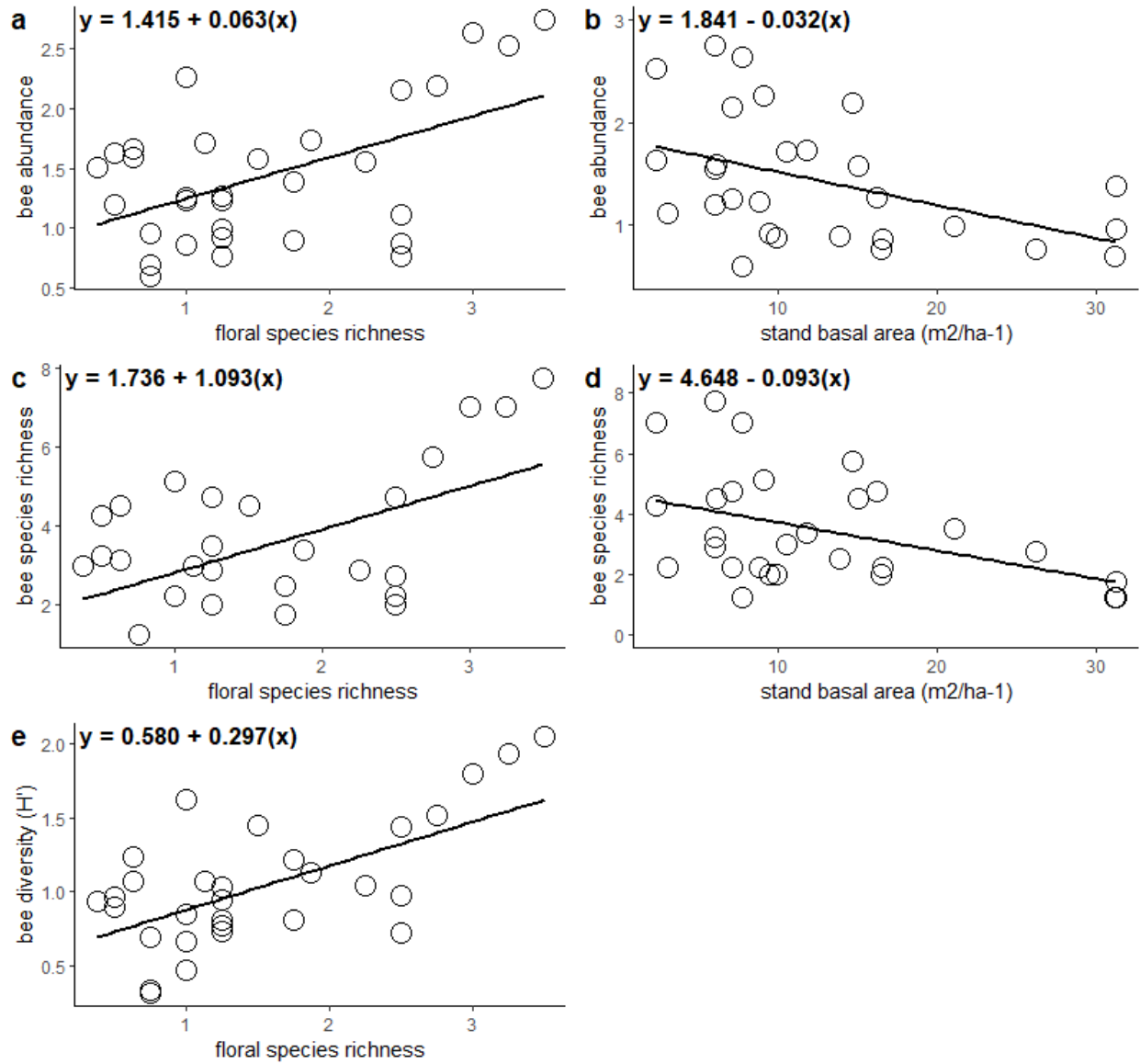


Figure 3.8. Linear models describing the relationship between bee abundance and (a) stand basal area and (b) floral species richness; bee species richness and (c) stand basal area and (d) floral species richness; and (e) bee diversity and floral richness. All regression models are significant at a Type I error rate of $\alpha = 0.05$.

CONCLUSION

Anthropogenic and natural disturbances have cascading impacts on native bee communities. Particularly, the mosaic of habitat types left on the landscape as a result of disturbance events leads to varying resource availability, further influencing bee community assemblages and site occupation. For example, we found high severity wildfire was associated with increases in both bee abundances and diversity. Within these stands we also found the lowest tree densities, highest floral resource availability, and highest amount of woody debris nesting material. This aligns with results in Galbraith et al. 2019a, where findings elucidated that increased fire severity led to increased bee site occupancy. These relationships suggest implications for forest management that can inform future management decisions. Here, we found that forest thinning treatments were a non-deleterious management method that can be used to achieve restoration goals, as well as alter nesting habitat availability for bees. Specifically, thinning can either provide additional woody-nesting material for above-ground nesting bees if debris is left on-site following treatment, or if woody debris is removed, bare soil availability is likely increased and promotes nesting substrate for below-ground nesting bees. Thinning is also associated with increased understory productivity, in terms of both plant abundance and diversity, because of increased light availability to the forest floor. This increases foraging resources for insect pollinators in general. Further, we found prescribed fire to be a beneficial management tool. Our results suggest that prescribed fire treatment led to immediate increases in floral diversity, likely driving observed increases in bee diversity within 1-year post-fire stands. Together, disturbance patches left by forest management methods contributes to the mosaic of habitat types across the landscape, as we observed unique assemblages associated with varying time-since fire which further contribute to bee β -diversity.

More specifically, managers can target specific habitat components to optimize bee biodiversity. Tree density can be decreased to promote understory floral communities, increasing bee activity. Evidence here supports floral resources are a primary driver for bee assemblages and site

occupancy, as across these studies we have generalized findings that illustrate stands with increased floral resource available also experienced increases in bee community metrics. This is further supported by Campbell et al. 2018, where prescribed fire usage enhanced plant diversity, leading to increases in bee abundance. Nesting habitat in the context of woody debris can also be manipulated, with or without thinning treatments, to promote certain bee taxa with trade-offs for below- and above-ground nesting bees. For example, our regression models (Fig. 2.8c) show a ~19% decline in bee species richness between coarse surface fuel loadings of 25 Mg/ha to 15 Mg/ha. Additionally, as we saw increased surface fuel loadings, we observed decreased floral abundances but increased floral richness (Fig. 2.3). High fuel loadings may suppress understory productivity by reducing forb growing space yet allows persistent or advantageous forb species to continue to establish. However, the threshold as to where high floral community productivity and optimal woody nesting availability lies is unknown and requires further exploration. Lastly, managers should also seek to maintain pyrodiversity on the landscape, including both mixed severities of wildfire disturbance and prescribed fire treatment, as each provides unique habitat with varying structures and each disturbance patch was associated with unique bee communities, with certain bees expressing habitat preference.

Several limitations of these studies should be considered when interpreting results discussed here. Unmeasured aspects of variability within study sites could strengthen understanding of factors influencing bee community dynamics. Abiotic factors such as mean site temperature, average precipitation or humidity, and windspeeds can impact both plant phenology and insect behavior (Fucini et al. 2014). Second, landscape factors drive distributions of insect populations at large scales. Incorporating spatial distributions of various land cover types and proximity to sample sites can improve models of bee species distribution that include comparisons of small- and large-scale factors. Finally, additional sampling methods may also be utilized to reduce bias when inventorying bee communities. Here we use blue vane traps, which are known to exhibit bias towards large-bodied bees (Geroff et al. 2014; Gibbs et al. 2017). Though passive sampling using blue vane traps offers opportunity to sampling large landscape network and are effective over short deployment periods,

supplementary sampling such as active netting or pan traps can ensure sampling of varying bee taxa (Rhoades et al. 2017).

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